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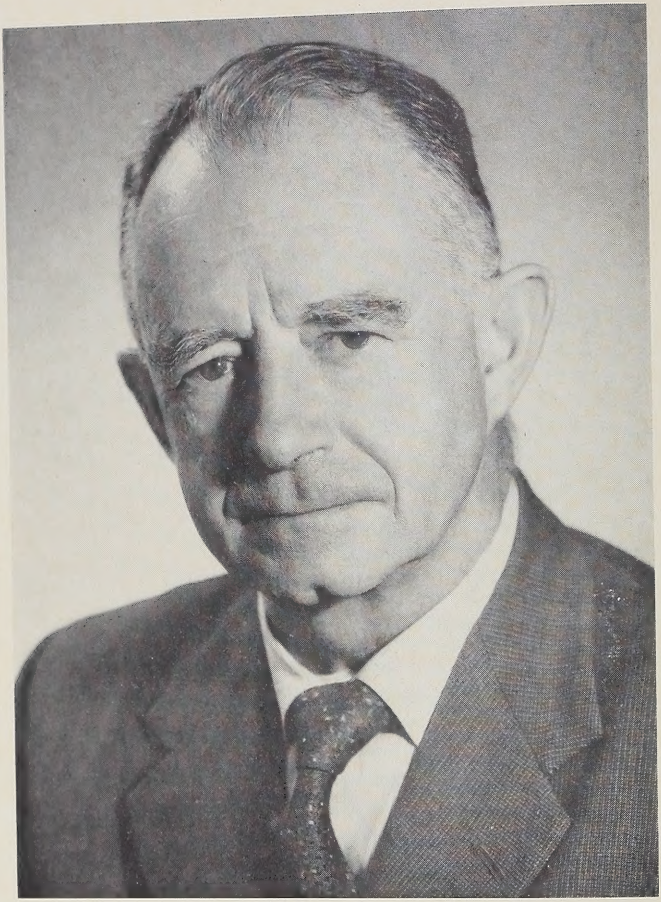

THIS VOLUME IS DEDICATED TO

Robert Allen Dyer (1900–   )

D.Sc., F.R.S.S. Afr.

(*Chief of the Botanical Research Institute and Director of the Botanical Survey of South Africa, 1944 to 1963*)

distinguished authority on the flora of Southern Africa with many valuable publications to his credit, particularly in connection with the succulent Euphorbieae, Crassulaceae, Stapelieae and other groups such as the Cycads and Amaryllidaceae, presently engaged on a complete revision of "The Genera of South African Flowering Plants", who has played a leading part in the major scientific societies, having been President of the South African Biological Society (1948) and of the South African Association for the Advancement of Science (1960) and whose contributions have greatly enhanced the status of Botany in South Africa.

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A CONTRIBUTION TO KNOWLEDGE OF PHRAGMITES (GRAMINEAE) IN SOUTH AFRICA, WITH PARTICULAR REFERENCE TO NATAL POPULATIONS

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Abstract

A study of populations of *Phragmites*, in Natal, revealed differences in vegetative structure, epidermal features, chromosome numbers, habitat preferences and distributional patterns, between *P. mauritianus* Kunth and *P. australis* (Cav.) Trin. ex Steud.

Some of these differences facilitate identification of the two species, especially in the field. The habitat preferences are significant in relation to ecological changes, particularly siltation, in swamps and estuaries.

Uittreksel

'n BYDRAE TOT DIE KENNIS VAN *PHRAGMITES* (GRAMINEAE) IN SUID-AFRIKA, MET SPESIALE VERWYSING NA DIE NATAL POPULASIES.

'n Studie van Natalse *Phragmites* populasies het die volgende feite aan die lig gebring: naamlik, dat *P. mauritianus* Kunth en *P. australis* (Cav.) Trin. ex Steud. van mekaar verskil ten opsigte van vegetatiewe-samestelling, epidermale-kenmerke, chromosoomgetal, habitatsvoorkeur en verspreidingspatroon.

Sommige van hierdie verskille vergemaklik identifikasie van die twee soorte in die veld. Hulle habitatsvoorkeur is betekenisvol ten opsigte van ekologiese veranderinge, in besonder ten opsigte van toeslikking in moerasse en riviermonde.

The reed, *Phragmites* Adan. (Gramineae, Arundineae) is common along river and stream banks in South Africa. Chippindall (1955) recorded *P. communis* Trin. and *P. mauritianus* Kunth for the Republic and stated that the former was widespread, the latter, without record from the Cape Province, was more tropical. The relative length and width of the glumes was considered the most reliable means of distinguishing between these species.

Clayton (1967), in considering the genus on a world basis, concluded that from among the "... very large number of species and infra-specific taxa ... described ...", three allopatric species should be recognized. All three, according to this author, are represented on the African continent. *P. karka* (Retz.) Trin. ex Steud. in Ethiopia, the Sudan and West Africa, with rare specimens in Kenya and Uganda. *P. mauritianus* Kunth in Tropical Africa, the northern limit passing through Ethiopia, the Sudan and the Congo; no southern limit being stipulated. *P. australis* (Cav.) Trin. ex Steud. = [*P. communis* Trin.] (Clayton, 1968), with subspecies *altissimus* (Benth.) Clayton limited to the Medi-

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terranean shores, the southern edge of the Sahara, Ethiopia and Kenya, and subspecies *australis* in temperate regions of both hemispheres (which would include South Africa). Clayton stressed that the three species "... cannot be readily separated by any single character," so that it is essential to assess the distinguishing features as a whole.

Undoubtedly both *P. mauritianus* and *P. australis* subspecies *australis* grow in Natal, but neither the glume parameters recommended by Chippindall, nor the broader plexus of distinguishing characters advocated by Clayton, nor other available keys such as that of Sturgeon (1954) relating to Rhodesian grasses, engendered full confidence in attempting to identify flowering herbarium specimens. Sterile material was even more uncertain.

As populations were readily available for study, a field and laboratory investigation was undertaken to determine whether living plants could be identified more easily than dried material, and whether additional criteria might be detected that would make distinctions between established taxa more conclusive. At the same time, attention was paid to variation within and between populations, and to the general ecological conditions under which plants grew, as far as these could be simply assessed. Lastly the distributional range, particularly in Natal, was recorded.

Study of Populations

A: *In the Field*

1. *Sampling. Phragmites*, in South Africa, flowers in late summer and autumn. During these seasons, populations were located, studied and sampled. The populations considered in detail were mostly in Natal, from the coast and midlands. Up to twenty stems (approximately three quarters in flower, one quarter sterile) from each population were dug out or cut close to ground level, then folded into presses to serve as reference samples for subsequent laboratory study. As far as possible, the stems taken represented specimens grading from the fringe to more deeply into a population, so as to cover a representative range of habitat conditions, but it was sometimes difficult to penetrate far where plants grew in water. Representative material (mature leaves borne at half to two-thirds the height of the flowering stem, well developed inflorescences, young axillary buds and roots) were fixed in recommended fixatives for subsequent floral, anatomical and cytological study.

In addition to initial location and study, many of the populations were re-visited at other seasons, so that observations could be made at different stages in the life-cycle. Also new populations from the Transvaal to the Cape were located from time to time and observations made. Herbarium specimens from widely differing localities were also examined for purposes of comparison with living plants and to supplement distributional records.

2. *Results of Gross Morphological Study.* Field study soon revealed that the species were distinct under natural conditions and could generally be recognized quite readily: especially was this so at the peak of the flowering season when inflorescences were numerous and in good condition.

FIG. 1.
Phragmites mauritianus: inflorescence.

FIG. 2.
Phragmites australis: inflorescences (note stem to the left with leaves, except the uppermost, arranged in a single plane.

The most conspicuous character of difference is undoubtedly the form of the mature inflorescence: lax and with drooping branches in *P. mauritianus* (fig. 1); more compact with straight or only very slightly drooping branches in *P. australis* (fig. 2). (The photograph reproduced in Chippindall, 1955: 228 is almost certainly of *P. mauritianus*). Clayton, 1967, referred to these

inflorescence differences in his key as follows: "... panicle often smaller, the lowest node usually few-branched, some of the branches bearing spikelets nearly to their base ..." (*P. australis*); "... lowest node of the panicle often many-branched in a whorl, the branches bare of spikelets for some distance from their base" (*P. mauritianus* and *P. karka*). The disposition of the spikelets on the branches largely governs the lax, or compact, appearance of the whole inflorescence, which character can be observed some distance from the population, and therefore serves as a valuable first clue to identification. Some provisos are necessary, however. With ageing, the several florets of each spikelet are shed, leaving the glumes persistent upon the inflorescence branches. Panicles of both species, at this stage, look considerably less compact than do the same panicles when many florets are undergoing anthesis. Within a population, flowering of plants is usually simultaneous, nevertheless some younger and some older inflorescences are always represented among a majority at peak of development. Thus representatives of similar age should be compared. In *P. australis* the uppermost culm leaf frequently sheaths the base of the panicle: this emphasizes the impression of its compactness and makes dissection necessary to see the arrangement of the lowest inflorescence branches. In both species, two nodes separated by only a short internode often mark the inflorescence base. Each node carries usually a single branch that is itself branched from almost the extreme base. The close proximity of the two nodes suggests a whorled arrangement that is not actually represented, so that Clayton's criterion of panicle branching often does not hold in South African specimens of *P. mauritianus*.

With emergence of the immature inflorescence and during subsequent flowering and fruiting, leaves dry and fall away progressively from the base of the culm upwards. The position of the abscission layer responsible for this loss provides another distinguishing character useful in the field. In *P. mauritianus* it develops in the leaf sheath immediately above the node from which the leaf arises, so that leaf sheath and blade are shed as a unit, leaving the internode bare with the axillary bud exposed (fig. 3). In *P. australis*, abscission takes place at the base of the leaf blade immediately above the collar, so that the blade falls leaving the sheath enveloping the stem and generally overlapping the internode and sheath above (fig. 4). This sheath has to be artificially removed before the axillary bud becomes visible. By time inflorescences are mature, flowering stems may have lost all but the uppermost six to five blades, but internodes, in the basal two-thirds, are clothed in persistent leaf sheaths. In *P. mauritianus*, by contrast, culms bearing mature inflorescences usually carry more than six leaf blades, but consist of naked internodes (often pinkish or purplish if habitat conditions are more extreme than usual) with lateral buds exposed in the middle region, the base bearing bract-like scale leaves only

FIG. 3.

Phragmites mauritianus: portion of flowering stem showing, below, leaf sheath abscising immediately above node; above, axillary bud exposed by leaf sheath already fallen.

FIG. 4.

Phragmites australis: portion of flowering stem showing overlapping persistent leaf sheaths: leaf blades already fallen as a result of an abscission layer developed at the junction of each blade with its sheath.

little better developed than are those of the rhizome. In *P. australis* the leaf blades persisting below the inflorescence frequently lie in a single plane (visible in fig. 2: culm on left) whereas this seldom if ever applies in *P. mauritianus*.

After flowering, culms of *P. australis* die back either to ground level or to the first side branches, if such are present, but expansion of the lateral buds in this species is unusual (a statement supported by Haslam, 1969a: 128; 1969b: 289) and seems attendant upon breakage or damage of the stem apex. In *P. mauritianus* the previous summer's flowering stems die back the following spring, but distally only, so that the major part of each culm remains photosynthetically active. These differences in growth pattern afford another means of distinguishing between the species in the field, for the complete die-back of usually unbranched stems in *P. australis* contrasts with die-back of the distal tips only of usually well branched flowering stems in *P. mauritianus*. Thus where populations have not been subjected to fire in the post-flowering period of winter to early spring (firing is a frequent happening in Natal), dead culms among densely produced new lateral innovations are a feature of populations of *P. australis*, but are lacking in *P. mauritianus*. Caution must be observed, however, for without careful scrutiny to detect evidence of firing, use of this single criterion as a means of species distinction can be misleading.

FIG. 5.
Phragmites mauritianus: axillary bud.

FIG. 6.
Phragmites australis: axillary bud.

The dormant axillary buds, themselves, differ in form (figs. 5, 6): the differences appear constant but are difficult to express accurately in words. Buds of *P. australis* are more markedly recessed into the nodal tissue than is the case with *P. mauritianus*, and are more nearly round in outline in face view

Fig. 7.

Phragmites mauritianus: left: apex of leaf sheath and base of blade showing ligule and tufts of fine white hairs on either side near sheath mouth (erect hairs behind ligule lacking); right: portion of ligule, in detail.

Fig. 8.

Phragmites australis: left: apex of leaf sheath and base of blade showing ligule and erect white hairs arising from behind ligule; right: portion of ligule with erect white hairs behind, in detail.

with a definite basal pediment that is absent in the more oval, usually larger buds of *P. mauritianus* (culms of approximately the same diameter should be compared). Outermost protective bud sheaths in both species are hairy marginally in the upper half, but hairs in *P. mauritianus* are more numerous and form a thicker, more conspicuous fringe. Another useful difference detectable in the field, lies in features of the ligule. In *P. australis* leaves near the apices of actively growing sterile shoots show well the long, erect, white hairs produced immediately behind the ligule. These are especially conspicuous when the leaf blade is folded back. In *P. mauritianus*, such hairs are usually either shorter, fewer and finer, or occasionally may be absent (figs. 7, 8, 9), and are always accompanied by shorter, finer more bunched trichomes at either side of the sheath mouth, in the position where auricles sometimes occur in other grasses. The long hairs behind the ligule in *P. australis* dry with age and break or fall away, as eventually do the shorter ones of *P. mauritianus*. Old leaves, or leaves below an inflorescence thus should not be examined for characters of the ligule.

Differences in leaf blade colour, texture and apex exist in the two species. These are usually clearly evident in Natal populations, especially when both

taxa grow in fairly close proximity and can be compared in the field. Blades of *P. australis* are glaucous blue beside the yellowish green of *P. mauritianus;* soft against the stiffer harder texture of the latter; they wilt and roll rapidly when detached, suggesting either greater water loss in a given time, or less ability to withstand equal loss without permanent damage; apices are far more gradually tapering and much longer acuminate in *P. australis* than in *P. mauritianus*, while reduced blades of the developing axillary shoots have soft apices in the former, but are pungent and penetrating in the latter. (Clayton, 1967: 115 also observed differences in leaf blade apex in the two species, expressing them as follows in his key "leaf blades . . . the tips filiform and flexuous . . . *P. australis*. Leaf blades . . . the tips attenuate, stiff or even pungent . . . *P. mauritianus*.") While these differences apply in Natal and further north where environments are sub-tropical, they are not as readily detectable in plants of the winter rainfall area of the south-western Cape Province. Firstly, it should be recalled that no natural stands of *P. mauritianus* are presently recorded for the

Fig. 9.

Phragmites australis: portion of leaf sheath from sterile aerial stem with leaf blade folded back to show erect white hairs.

Fig. 10.
Phragmites mauritianus: portion of population fringing Umgeni River at Morton's Drift, showing profuse branching of aerial stems.

Cape Province, so that populations of both species growing under conditions of winter rainfall are not available for comparison. Secondly, the dry summer season seems to produce (under certain ecological conditions of intermittent water supply at least), greener rather than more bluish leaves in *P. australis* and more effectively pungent reduced leaf blades to axillary shoots than is the case at less southerly latitudes. There are possibly other habitat factors that

may result in the development of sharper, firmer apices to leaves of axillary shoots in *P. australis* (see Haslam 1969c: 707 with reference to salinity). Further field observation of *P. australis* in the Cape Peninsula and in arid South West Africa is needed.

FIG. 11.
Phragmites mauritianus: expanded axillary shoot showing pungent apices to leaf blades and tufts of fine white hairs at sheath mouth.

Haslam (1969a) in studying *P. australis* = [*P. communis*] in the British Isles and Malta, recognized the occurrence of four different stem types in this plant, namely, horizontal rhizomes (the juvenile type responsible for renewing the stand), vertical rhizomes (which bear aerial shoots), aerial shoots (the photosynthetic, potentially flowering, short lived stems) and legehalme (the non-rigid runners of indefinite growth produced most commonly in new communities or in brackish water). All four stem types are represented in Natal plants of *P. australis*. It is the mature stem type, the aerial, short-lived, photosynthetic, potentially flowering stem that has been dealt with in this paper up to now. Legehalme were commonly produced when plants were colonizing newly developed mud banks (Ward 6597), occasionally developed in populations growing in brackish water (Ward 6594: 6598). Lengths for legehalme exceeding eleven metres were measured, which agrees with Haslam (1969a: 129), who reports their lengths as greater than those of any other stem type, ". . . frequently reaching 10 m". In other respects, too, the legehalme of Natal plants of *P. australis* agree with those described by Haslam for plants of the northern hemisphere.

The white, horizontal rhizomes are generally dorso-ventrally flattened;

FIG. 12.
Phragmites australis: legehalme developed where plants are establishing themselves on clayey mud: Durban Bayhead, June, 1970.

sometimes they flex above ground level to form a photosynthetic knee (Ward: 6764). Adventitious roots radiate in all directions from subterranean nodes, but only descend from nodes on or close to the soil surface.

In *P. mauritianus*, legehalme have never been observed, but the other stem types are the same as in *P. australis*, except that type for type and branch sequence for branch sequence they are more robust.

In the Natal populations of both species studied in detail, young inflorescences became evident above the apical culm leaves in December. Anthesis was at varying times from March to July, mainly April to June inclusive, while fruit was dispersed (in *P. australis*) over the period April to July inclusive. In *P. mauritianus* heads were apparently fruiting from (March) April-June (July), but whether viable seed was actually dispersed is open to question since laboratory study of representative heads yielded no perfectly formed mature fruits.

3. *Results of Ecological Study*. No more than observational notes and suggestions for further study are given here, for it was not possible to undertake experimental investigation into the habitat conditions favoured by each species.

From observation it became apparent that the two species have different habitat requirements. This is of particular interest, since, in Natal at any rate, populations of each species are often to be found in the same general locality. Sometimes this is the case inland: frequently it is so at the coast where populations may occur juxtaposed, or almost so, or where plants of *P. mauritianus* may surround, or partially surround, or penetrate as local minor intrusions, extensive stands of *P. australis* that are otherwise pure.

P. australis grows in swamps or vleis, or in other places with restricted drainage such as river back-waters more or less isolated from the main stream, or in standing water up to 70 cm deep, often forming extensive reed swamps. Plants extend into inter-tidal estuarine areas, especially where the salinity is reduced by the inflow of fresh water. (Measurements of salinity, from $0{\cdot}3\%$ after heavy rains, to $2{\cdot}1\%$ after neap tides and $3{\cdot}1\%$ after spring tides, were recorded for Isipingo populations during the present study using the specific gravity method. High salinities were usually not of long duration, however.) The soils favoured were generally moist organically rich sand, or clayey sand and mud. Occasionally plants occupy steep mesoclinal banks where there is no visible water: here the soils are always clayey rather than sandy.

P. mauritianus, on the other hand, occurs in riverine situations, often flood plains preferably with well-drained, often sandy soils and permanently flowing or frequently moving water, or in other moist situations especially where there has been recent disturbance of the habitat. The horizontal rhizomes readily penetrate sandy alluvial deposits, so that plants are often the first perennials to re-colonize flood disturbed river banks. Only rarely does the species extend

to where plants may be affected by the extreme high water of an equinoctial spring tide. Frequently local populations grow well away from visible or near surface water. Such situations may be north or east-facing and thus more xeric than those favoured by *P. australis*, with soils sandy rather than clayey.

Where plants of *P. mauritianus* partially surrounded, or extended as local penetrations into, populations of *P. australis*, investigation showed disturbance of the habitat originally occupied by *P. australis* in the areas invaded (particularly in respect of soil/water relationships), thus affording suitable conditions for colonization by *P. mauritianus*. Such disturbance was either due to the deposition of soil by flooding or was the outcome of man's activities. In one case, at Isipingo, the only penetration into a population of *P. australis* by *P. mauritianus* was where a drainage exit from the swamp had been constructed. Where disturbance resulted in impeded drainage or the deposition of clay soils, *P. australis* was occasionally found to have re-established itself. Thus in localities where both species are represented, it is edaphic conditions that seem to control the patterns of distribution. It is at present no more than speculation to suggest that oxygen levels within the soil and water of the habitat may be limiting in determining where *P. mauritianus* can survive. Certainly this species seems to require better drainage, and thus aeration of the substrate, than does *P. australis*. It also seems better able to withstand drier conditions, but this may apply only under sub-tropical conditions, for in the south western Cape during the dry summer months, *P. australis* may be seen flourishing in dry (at least superficially so) water courses.

Because of these different habitat requirements, the distributional pattern of the two species is frequently revealing in gaining understanding of the pattern of environmental change within an area. Particularly is this so along the coast and along some river courses where isolated relict patches of *P. australis* indicate the earlier presence of extensive reed swamps or poorly drained vlei areas. At Midmar Dam, in April, 1968, below the sluice-gates of the main dam wall a portion of a population of *P. australis* was still standing in what had been a vlei area. Slightly below this, evidence of the dumping of large mounds of soil into this vlei was still apparent. Much of the dumped soil had already been colonized by *P. mauritianus* which was flowering, as was *P. australis*. With disturbance of the habitat, evidence suggests that plants of one, or other, species may eventually disappear leaving little, if any, evidence of previous prevailing conditions. Nothing definite is known of the time that might be involved for such changes to be completed, however.

Physio-ecological water relationships of intact plants of each species may repay investigation. The inter-play, if any, between pattern of leaf abscission, rate of water loss from the plant as a whole unit, and survival within a particular type of habitat, especially where seasonal fluctuation in water levels occurs, are

not understood. It may be that plants of *P. australis* with their habit of leaf blade abscission and complete die-back of post-flowering culms are less demanding of available water during the winter season than are plants of *P. mauritianus* in which post-flowering stems remain leafy and thus active transpirationally. On the other hand, the harder leaves of the latter may, perhaps, transpire less water than those of the former, and thus be hardly more demanding of available water during the unfavourable season than the non-leafy stems of *P. australis.*

In plants of *P. australis* growing where saline conditions prevailed and where the habitat had been infilled with sandy clay (Ward 6763), adventitious roots developed from the horizontal rhizome were greatly swollen, obviously serving a water storage function. Such markedly swollen roots have not been found in other habitats, nor yet at all in *P. mauritianus*, but it may be that the adventitious roots do serve as a useful water reserve in certain environments.

Haslam (1969a, b and c) has drawn attention to aspects of ecological behaviour in plants of *P. australis* growing in northern latitudes that are of some significance in southern populations and which may well operate within plants of *P. mauritianus* also.

This author has shown the growth pattern for northern populations of the former species to be as follows. Underground horizontal rhizomes grow during autumn. As a result of internal control, each changes into a vertical rhizome which, when internal dormancy ceases and provided the external environment is generally favourable, develops in spring into an erect, aerial, photosynthetic, potentially flowering stem. On all parts of this system, axillary buds are produced one at a node. On horizontal and vertical rhizomes, buds may be laid down almost all the year round, but remain underground while internal dormancy operates. This ceases in spring, when, provided temperatures are not too low and thus in turn limiting, the buds emerge to develop into aerial stems. The period of emergence is relatively rapid and once begun continues without re-establishment of internal dormancy even if low temperatures again obtain. Emerged buds and aerial stems are frost sensitive, whereas underground rhizomes and legehalme are not.

Fire, provided sufficiently severe to sever the aerial stems, breaks internal dormancy, and bud emergence, provided environmental temperatures are not too low, commences about a month after firing. Severe fires which scorch the ground may delay bud emergence for two months, possibly because of direct influence on the rhizomes. Cutting of rhizomes also causes breakage of internal dormancy, thus such treatment (ploughing) may hasten bud emergence. Cutting of aerial, photosynthetic stems late in the growing season has little effect on the population, but early in this season such treatment prevents the laying down of adequate food reserves and thus depletes subsequent growth. Haslam states

that early spring/summer cutting of photosynthetic stems is consequently the best (simple) means of controlling northern populations of *P. australis*.

The general growth pattern in southern populations of both species is the same as determined by Haslam. Because of sub-tropical maritime climates, the coastal southern African populations in particular, as far south as the western Cape, will be little influenced by frost, but cold may well have an effect in delaying emergence of aerial shoots in inland populations, especially those near the mountains. Fire is another factor which undoubtedly influences almost all southern African populations either regularly or occasionally (with the possible exception of South West African stands). In Natal, a dense coverage of aerial shoots emerges after firing, but the time lapses between firing and visible growth of young emerging shoots for individual populations were not precisely noted.

Haslam also mentions the adverse effect on emergence of aerial shoots of lack of flooding and dry environmental conditions, and of salinity upon intercalary growth, which influences internodal length producing shorter stems. Leaves, under these conditions, tend to be more markedly xeromorphic (more pungent apically). Ranwell and co-workers 1964: 637 concluded from work done in southern England that mature plants of *Phragmites* could not survive where the soil solution at 10 cm depth exceeded 1·2% chlorinity (2·0% salinity), (presumably for any length of time—our proviso). All these points should be kept in mind when considering southern populations particularly in relation to damming, siltation, and changes in estuarine environments that may be the direct or indirect outcome of natural or man-influenced environmental change.

B: *In the Laboratory*

1. *Spikelet Morphology*. Clayton's (1967) work and comments formed the basis of a preliminary survey carried out to determine features of spikelet structure likely to prove most reliable and easy to use in helping to distinguish between *P. australis* and *P. mauritianus* in South Africa. Lengths and widths of glumes and first (lowest) lemma seemed most promising, with number of florets to the spikelet affording another possible criterion not previously in use. No other features of the spikelet that had not already been considered by other workers warrented assessment.

With these guiding ideas in mind, field samples were studied, each group of approximately fifteen flowering stems (fewer in the case of Umbogintwini) being regarded as representative of a population and providing thirty spikelets taken at "random" for scoring.

Despite the greater number of florets often present in spikelets of *P. australis*, it soon became apparent that this parameter could not be included among re-

TABLE 1
Populations of *Phragmites mauritianus* studied in detail

Code	Grid Ref. & Specific Locality	Collector's Name & No.	Habitat Conditions
Peattie's Lake	Natal—2930 (Pietermaritzburg): Umgeni Valley (-AD): small streamlet to north of Peattie's Lake	Gordon-Gray, K.D. 6158	in clayey mud of bank and in moving water, up to c. 1 m in depth, of streamlet.
Morton's Drift	Natal—2930 (Pietermaritzburg): Umgeni river: Morton's Drift (-AD) near Otto's Bluff	Gordon-Gray, K.D. 6157	in clayey mud, among dolerite boulders of bank and in moving water of Umgeni river.
Albert Falls	Natal—2930 (Pietermaritzburg): Umgeni river near Albert Falls (-AD)	Gordon-Gray, K.D. 6159	in dry grassveld: fairly low-lying: inundated under flood conditions.
Midmar	Natal—2930 (Pietermaritzburg): Umgeni river, Midmar Dam: (-CA) immediately downstream of main dam wall	Gordon-Gray, K.D. 6160	in doleritic soil of infill into vlei originally occupied by *P. australis*: plants c. 2 m above river level.
Mpushini Valley	Natal—2930 (Pietermaritzburg): Ashburton, Mpushini Valley (-CB) 29°40′S 30°28′E	Ward 6586	in clayey loam (ex dwyka tillite) on floor of small, dried dam c. 2,000 ft.
Mlazi River	Natal—2930 (Pietermaritzburg): Mlazi River: (-CD) on main road between Eston & Umlaas Rd. 29°46′S 30°31′E	Ward 6587	in alluvial loamy clay on and between boulders at side of river from 1·2 m above current water level to wet clay at river's edge.
Hammarsdale	Natal—2930 (Pietermaritzburg): Hammarsdale (-DA) off main Durban-Pietermaritzburg road	Gordon-Gray, K.D. 6155	in sandy dry soil on hillslope above small streamlet (no water visible)
Isipingo	Natal—2930 (Pietermaritzburg): Isipingo (-DD) 29°59′S 30°57′E	Ward 6584	in moist silty sand alluvium on bank of upper estuary, above tidal range except at spring tide when bases covered at high water c. 1 m alt.
Isipingo Flats	Natal—2930 (Pietermaritzburg): Isipingo Flats (-DD) 29°59′S 30°56′E	Ward 6590	in alluvial, slightly silty sand in former flood diversion canal c. 2 m alt.
Karridene	Natal—3030 (Port Shepstone): Mzimbazi Valley, W. of Karridene (-BB) 30°07′S 30°49′E	Ward 6593	in alluvial sand on floodplain of stream, in thicket. c. 4·5 m alt.

TABLE 2
Populations of *Phragmites australis* studied in detail

Code	Grid Ref. & Specific Locality	Collector's Name & No.	Habitat Conditions
Estcourt	Natal—2929 (Underberg): Estcourt (-BB) beyond township on road to Tabamhlope	Gordon-Gray K.D. 6279	in fine alluvial mud: low-lying flat area (no water visible, but water would stand after rain): c. 100 m from streamlet in grassveld.
Cedara	Natal—2930 (Pietermaritzburg): near Cedara College (-CB) stream between main road and railway	Gordon-Gray, K.D. 6282	in alluvial mud: flat area extending beyond banks of streamlet: plants in standing water.
Eston	Natal—2930 (Pietermaritzburg): Eston (-DC): junction of road D 362 with main Eston-Umlaas Rd.	Ward 6588	wet clay of swamp: low-lying flat area on both sides of water course in flat valley—c. 670 m alt.
Bluff	Natal—2930 (Pietermaritzburg): Durban Bluff (-DD) on flats on road to Wentworth Hospital	Gordon-Gray, K.D. 6156	in sandy soil: flat low-lying area (no water visible, but water would stand after rain): c. 1-2 m alt.
Isipingo Flats	Natal—2930 (Pietermaritzburg): Isipingo Flats (-DD) 29°58′S 30°56′E	Ward 6589	in red sandy soil of built-up road bank, plants growing through infill from former swamp: originally in clayey, fine sandy silt on alluvial plain.
Isipingo Beach	Natal—2930 (Pietermaritzburg): Isipingo Beach (-DD) 29°59′S 30°56′E	Ward 6597	in bush-cleared and levelled low-lying area in alluvial sand with humus and in clayey sand infill: c. 1 m alt.
Umbogintwini	Natal—3030 (Port Shepstone): Umbogintwini Lagoon (-BB) extremity of Golf Course 30°00′S 30°56′E	Ward 6596	in moist, alluvial silty loam, in depression on floodplain of upper estuarine lagoon, recently shallowly inundated: c. 1 m alt.
Umtamvuna	Natal—3130 (Port Edward): Umtamvuna river (-AA) 31°04′S 30°11′E	Ward 6755	in sand and mud at edge of estuary extending into water: c. 1·5 m alt.
Mzamba	Transkei—3130 (Port Edward): Pondoland, Mzamba (-AA) 31°06′S 30°10′E	Ward 6747	in beach sand at edge of estuary: c. 3 m alt.
Haven	Transkei — 3228 (Butterworth): mouth of Bashee River (-BD)	Gordon-Gray J.L. 862	in sand and mud under estuarine conditions, extending into water.

TABLE 3

Phragmites mauritianus and *P. australis*: some spikelet parameters of populations sampled in the field (figures derived from 30 spikelets from each population listed in tables 1 and 2)

	P. mauritianus (for 300 spikelets)	*P. australis* (for 300 spikelets)
Lower glume length in mm:		
extremes	2·0—4·8	3·1—7·0
mode	3·0	5·0
mean	3·3	4·8
Upper glume length in mm:		
extremes	3·0—5·7	5·0—9·2
mode	4·0	7·0
mean	4·2	7·0
First (lowest) lemma length in mm:		
extremes	4·7—10·0	7·5—15·0
mode	8·0	11·0
mean	7·3	11·3
Sum of lengths of lower and upper glume and lowest lemma in mm	10·2—19·7	18·3—27·0

liable indicator characters by which to distinguish the species. Firstly, there is overlap in floret number per spikelet: secondly, fragmentation of the rachilla from the apex downwards commences soon after anthesis of florets and is rapid after drying out, so that only comparatively young inflorescences showed full number of florets.

Measurement of glumes and first lemma revealed that ratios of width to length of these organs showed overlap between the taxa. Lengths also showed overlap, this being minimal in the case of the upper glume. When lengths for these three organs were summed for individual spikelets, the overlap persisted but was slight. This parameter and upper glume length were thus regarded as the most convincing spikelet characters by which to distinguish the taxa, especially when working with herbarium specimens.

Extremes, modes and means for lower and upper glume length and first (lowest) lemma length for thirty spikelets from each of the twenty populations listed in tables 1 and 2 were recorded. Since results were remarkably uniform and showed no significant variation in relation to habitat or locality, only the extremes, modes and means for all 300 spikelets measured within each species are given in table 3. (Figures for individual populations are available from one of the authors, KDGG, should they be required.) To gain evidence of variation in size of spikelet parts within populations distributed over the remainder of the sub-continent, parameters for thirty spikelets within each species, each spikelet taken from an herbarium sheet from a different locality, were measured.

Extreme lengths for these samples were well within extremes recorded for Natal populations.

Clayton (1967 and 1968) recognized within *P. australis*, subsp. *australis* from temperate regions of both hemispheres (thus including S. Africa), and subsp. *altissimus* for the large Mediterranean form. The latter, apart from its greater height and larger panicles, was distinguished (albeit "... rather imperfectly ...", as the author himself states) on upper glume shape and apex. Clayton also mentioned that the few tropical American specimens he had examined also appeared to fit this subspecies. Some S. African populations (Ward, Isipingo 6574 and Isipingo Flats 6589), as well as some herbarium specimens, particularly from the Cape Province and Orange Free State (for example Paterson 1043 BOL; Steyn 49 NBG) fit the glume requirements for this variety.

In view of the possibility that Clayton's subspecies is also S. African and thus not geographically separate from subsp. *australis*, no emphasis is placed on intra-specific categories.

2. *Leaf Anatomy*. Metcalfe (1960) urged caution in the placing of too great emphasis upon differences in leaf anatomy in the identification of closely allied species. No reminder of the close relationship between *P. mauritianus* and *P. australis* is necessary, so the differences in the anatomy of their leaf laminae, as seen in transverse sections and in the abaxial epidermides, are given with this warning in mind. The details may, nevertheless, assist those who are occasionally called upon to identify sparse, dry, leaf fragments or field populations not yet in flower: they may perhaps help, too, by adding to overall knowledge of anatomical variation in one of the world's most widely distributed angiosperms (*P. australis*), and in further elucidating relationship of the phragmitiform grasses within Gramineae, a problem that as yet has not been conclusively resolved.

Leaves from the twenty populations studied in the field were sectioned and epidermal tissues stripped. Mature leaves of approximately the same age were used (usually the fourth leaf from the apex of a sterile stem: only fertile stems were available for Umbogintwini). Preparations were made from midway along each blade. Staining was uniform for preparations of the same type.

T. S. Lamina. All laminae sectioned showed agreement in main structural features with Metcalfe's (1960: 385) description for [*P. communis*] = *P. australis*, so this account is taken as standard for both species. The keel, which in the S. African leaves of both species, was far less well developed with less parenchyma between abaxial vascular bundles and adaxial epidermis than in the illustration referred to for *P. australis* (Metcalfe, 1.c. fig. XIII, 3), was the most striking point of difference.

The several layers of palisade cells on the abaxial side of the leaf described for *P. australis*, were well defined in laminae of *P. mauritianus* also: in addition rather well defined palisade cells occurred adaxially as a rule. Metcalfe did not mention invaginated walls in any of the mesophyll cells, but in South African specimens these were well defined, especially in *P. mauritianus*, in fairly large cells situated between the abaxial epidermis and the bulliform cells. If these are arm cells, recorded so far only for Bamboos and members of Oryzeae (and there seems no immediate reason why they should not be so regarded), do they reflect closer relationship between *Phragmites* and the Bambuseae and Oryzeae than is presently considered probable?

Early study suggested that differences in number of vascular bundles between each pair of larger ones, outline shape of the small bundles (parenchymatous outer sheath included), and number of cells comprising this sheath, might be consistent for each species and might thus provide additional characters of distinction between them, but examination of all representative populations showed overlapping ranges of variation. The straightness of ad- and ab-axial surfaces in *P. mauritianus*, did, however, contrast consistently with the shallow ribs and furrows of comparable surfaces in *P. australis*. Extremes in some characters of lamina anatomy are illustrated in plan in fig. 13 a, b, and in detail in figs. 14, 15 but, as has been stated there is a range in each taxon resulting in overlap between these extremes.

Abaxial Epidermis. Metcalfe's (1960: 385) description for *P. australis* was valid for South African plants, except that walls of the long cells between the veins were thick and pitted rather than thin, a feature even better developed in *P. mauritianus* (fig. 16a).

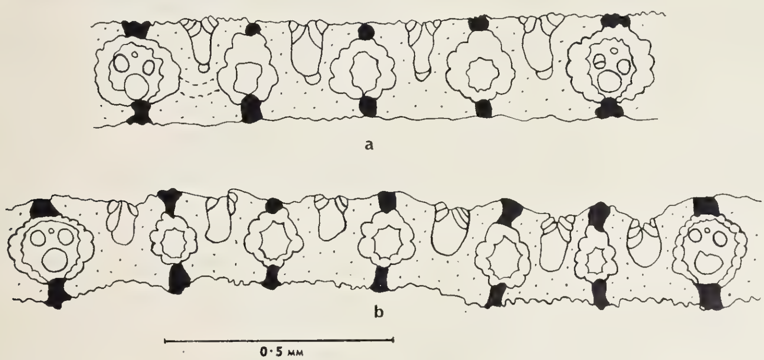

Fig. 13.
Anatomy of leaf blade in plan: a. *P. mauritianus;* b. *P. australis.*

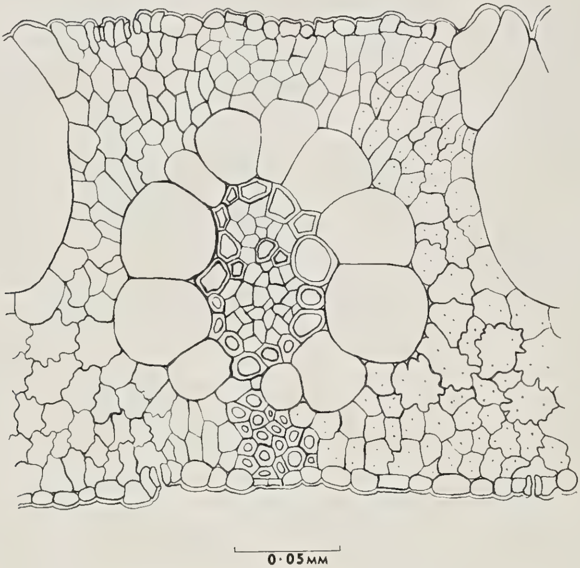

Fig. 14.
Phragmites mauritianus: portion of leaf blade in detail.

Apart from differences in disposition of the short cells in the stomatal bands (a cork and a silicified cell paired in *P. australis;* often only a solitary silicified cell in *P. mauritianus*), distinctions in abaxial epidermal structure between the taxa lay in the nature and disposition of the dermal appendages. Micro-hairs (fig. 16b) were readily detected on all leaves of *P. mauritianus* studied, being situated in those parts of the intercostal zones lying between the stomatal bands and the veins, and occasionally in the stomatal bands, but were *never* seen on leaves of *P. australis* as Metcalfe (1.c) also reports. This difference might not be meaningful in species diagnosis, in the light of variation observed for *Cortaderia selloana* by Metcalfe and Clifford (1968: 490), but it is certainly of interest in regard to the taxonomic relationship of the phragmitiform grasses within Gramineae. Leaves of *P. mauritianus* bore rows of prickle hairs as out-growths from epidermal cells above the veins. These sometimes varied markedly in size from one vein to the next on the same leaf, the largest bearing elongate, pointed apices almost the length of the cell itself (Isipingo Flats; Mlazi). No prickle hairs were seen on leaves of *P. australis*, but over the veins unpointed prickles of the type illustrated for *Arundo donax*

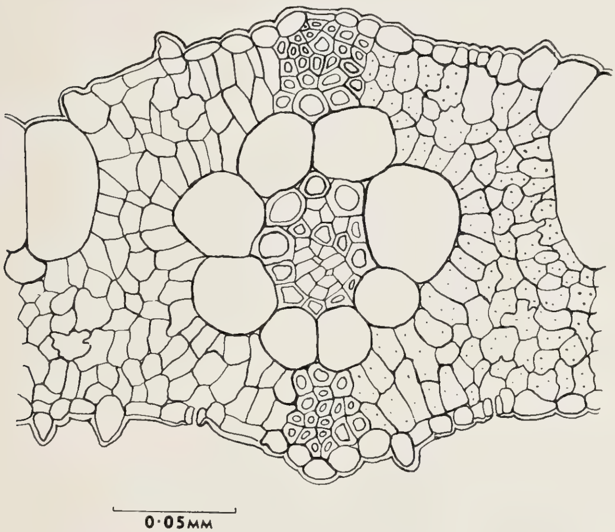

FIG. 15.
Phragmites australis: portion of leaf blade in detail.

(Metcalfe, 1960: fig. VI, 6) were frequent and somewhat variable in size, but much more uniform in dimensions than were the prickle hairs of *P. mauritianus*. On leaves of *P. australis* hooks were frequent in the intercostal zones, commonest among the stomata, almost invariably paired with a cork cell, but occasional also between the stomatal bands and the veins. On leaves of *P. mauritianus* hooks were occasional in the last named position, but almost, or entirely, absent from among the stomata.

Adaxial Epidermis. The only point worthy of note was that microhairs and prickles occurred at intervals fringing the rows of slightly sunken bulliform cells in *P. mauritianus*, whereas only hooks were found in this position on leaves of *P. australis*.

3. *Chromosome Number.* Counts of somatic chromosomes carried out on tissue of young axillary shoots developed on aerial stems gave n = 48 for *P. mauritianus* (two populations counted, Pietermaritzburg and Hammarsdale) and n = c. 96 for *P. australis* (two populations counted, Durban and Karridene).

Avdulov (1931) (see Darlington and Wylie, 1961) cited both these numbers

for *P. communis*, as did Bor, 1960: 416 for *P. communis* var. *communis* in India.

From the literature no record of chromosome number for plants identified as *P. mauritianus* could be traced. Can it be that material of this species was included among that of *P. communis* when counts were made, as in the past the distinction between them was not always recognized? This is no explanation for Bor's counts, since *P. mauritianus* is not recorded for India.

When time permits, further counts on Natal and South African populations must be carried out to determine the full range of somatic numbers represented. The populations investigated so far are not ideally representative in that both within *P. australis* were coastal, both within *P. mauritianus* were from further inland. For the genus *Phragmites*, however, it seems reasonably conclusive that x = 12 or 6. (Bews 1929 cites Tischler, 1927 as recording 2n = 18 for [*P. vulgaris*] = *P. australis:* see also Stebbins, 1958: 171.)

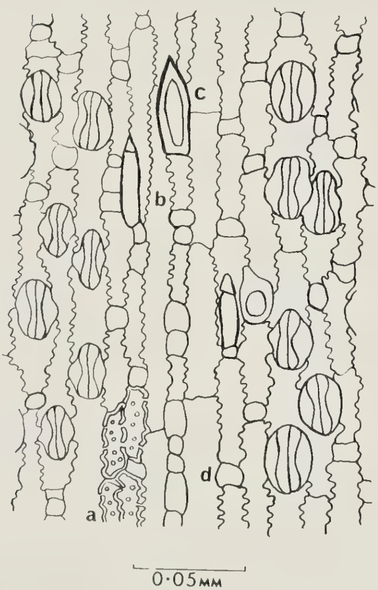

Fig. 16.
Phragmites mauritianus: portion of abaxial epidermis of leaf blade:
a. long cells showing thick, pitted walls. b. microhair. c. prickle hair. d. silica cell.

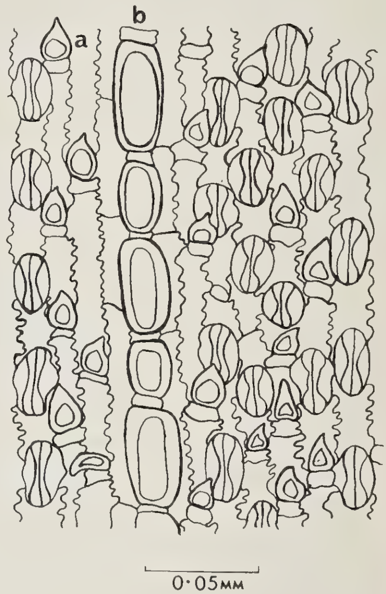

Fig. 17.
Phragmites australis: portion of abaxial epidermis of leaf blade:
a. hook paired with cork cell. b. unpointed prickles in portion of row of cells over vein.

Distribution

Present distributional records have been based on plants collected by both authors, and on herbarium specimens named against presently recorded differences between the taxa. In how far known records really express the situation in nature is questionable: the reasons for this are two-fold. Firstly, *P. mauritianus*, growing as it does where there has been some disturbance of the habitat, and often where conditions are drier, may partly or completely fringe populations of *P. australis*. Thus plants of one taxon may have been first to the hand of the collector, who unaware of differences between the species, may have failed to record the presence of both. Secondly, the ubiquitous presence of *Phragmites* wherever the authors have travelled since commencing this survey (thus becoming conditioned to looking for plants), has suggested that the genus is more widespread throughout the sub-continent than records show.

Fig. 18a.
Phragmites mauritianus: map showing known distribution in Natal.

Fig. 18b.
Phragmites australis: map showing known distribution in Natal.

Note: in the above maps one dot has been placed centrally in each magisterial district from which the species is known.

Natal. The known distribution in Natal of *P. mauritianus* and *P. australis* is shown in figs. 18a and 18b respectively. Both taxa are especially well represented along the coast. Ward 6757 from the Mpenjathi river, approximately

16,000 m (10 miles) north of Port Edward is the southernmost record for the latter species, whereas *P. australis* occurs under estuarine conditions at the mouth of the Umtamvuna river (the north bank being the Natal border) and into the Transkei. Apart from this, the distributional patterns hardly differ. Population study suggests, however, that *P. australis* is the "older" established inhabitant, long-settled wherever suitable habitat conditions prevailed; only now being challenged and sometimes ousted, by what appears a more "aggressive", tropical competitor undoubtedly aided by the siltation of lower lying water courses that is the outcome, in part, of natural denudation, but mainly of man's mismanagement of land at higher altitudes.

The familiarity of the Zulu and Xosa people with the reed, "emhlanga", is reflected in the names of some of the rivers and villages in Natal and the Transkei.

South Africa. Over the remainder of the sub-continent the distributional pattern is yet more uncertain. Evidence is reasonably convincing that natural populations of *P. mauritianus* are not represented in the Cape Province, but it is a possibility that isolated ramets may have been planted there by human agency. This species, which is widespread in Rhodesia, Swaziland, the Transvaal (presumably Moçambique, though no records for this country have been verified in course of the present work) and Natal, is predominantly northern and eastern.

P. australis, on the other hand is southern and western, being well represented in the Cape Province and South West Africa. It is eastern also, as the frequency of Natal coast populations demonstrates. Its detailed distributional pattern further north is unclear, nor are its northern limits in the continent accurately established. It is difficult to believe, for instance, that the species is absent from Swaziland, while occurring in Rhodesia. Any collections of specimens that will help elucidate distributional limits will be greatly appreciated by the authors.

Conclusions

To some extent the present study has served to emphasize differences between the two taxa already recorded by previous authors (Hubbard, 1937: Clayton, 1967). In addition it has revealed further points of difference especially in populations in the field, so that on the basis of deeper knowledge of the plants from a wider range of aspects, identification has become easier.

The present study has also shown that while habitat conditions do modify some features of morphological form, the pungency of apices to leaves of axillary buds in particular, under the sub-tropical to warm-temperate environments prevailing in Natal and associated areas, populations and the plants of which

they are composed, are clearly referable to one or other taxon. No evidence was obtained of plants or populations that were intermediate.

The further morphological and the anatomical differences disclosed, the habitat preferences revealed, and the more southern distribution of *P. australis*, all support the established concept that two taxa are represented. Absence of putative hybrids, sympatric association without loss of identity, and differences in ploidy are all suggestive of lack of gene exchange between them. This apparent genetic isolation, if eventually demonstrated experimentally, will provide irrefutable supporting evidence for the application of specific rank to which category both entities are already assigned.

Keys to Species

1. *For use in the field*

Leaf blade and sheath deciduous: shed from the stem by an abscission zone developed at the base of the sheath: internode thus eventually naked with axillary bud exposed (most readily seen in the lower half of flowering stems). Axillary bud hardly recessed into stem tissue, oval without a basal pediment. Mature stems usually bearing one to several expanded axillary shoots with leaves with pungent apices. Leaf blades to mature stems yellowish green, hard, not rolling soon after detachment from sheaths, apices attenuate, firm. Panicles lax with markedly drooping branches, at maturity not invested by the uppermost stem leaf . . . . *P. mauritianus*

Leaf blade only deciduous: shed from the stem by an abscission zone developed at the junction of sheath and blade: internode and axillary bud thus persistenly invested by the leaf sheath (most readily seen in the lower half of flowering stems). Axillary bud (when exposed by artificial removal of sheath) recessed into stem tissue, round, with basal pediment. Mature stems usually lacking expanded axillary shoots (except when stem apex previously damaged). When axillary shoots are present, apices to the leaf blades are firm, but never pungent. Leaf blades to mature stems bluish, rolling soon after detachment from sheaths, apices long filiform, flexuous. Panicles compact, branches slightly drooping, at maturity usually invested by the uppermost stem leaf . . . . *P. australis*

2. *For use in the herbarium*

Upper glume 3·0—5·7 mm long. Sum of lengths of lower glume, upper glume and first (lowest) lemma 10·2—19·7 mm. Mature leaves hard, apex attenuate, firm. Abaxial epidermis of leaf blade with scattered outgrowths in the form of: (1) prickle hairs over the veins, (2) microhairs between the stomatal bands and the veins (fig. 16) . . *P. mauritianus*

Upper glume 5·0—9·2 mm long. Sum of lengths of lower glume, upper glume and first (lowest) lemma 18·3—27·0 mm. Mature leaves soft, apex long filiform, flexuous. Abaxial epidermis of leaf blade with scattered outgrowths in the form of: (1) unpointed prickles over the veins, (2) hooks between the veins, most frequent amongst the stomata, each hook usually paired with a cork cell (microhairs have never been observed) (fig. 17) *P. australis*

Summary of the More Important Differences between the Species

P. mauritianus	*P. australis*
Legehalme (non rigid runners of indefinite length) never observed	Legehalme produced by plants colonizing exposed mud banks, or growing in brackish water
Horizontal rhizomes terete	Horizontal rhizomes somewhat flattened dorso-ventrally
Mature photosynthetic leaf blades yellowish green, hard, not rolling immediately on detachment from sheaths, apices attenuate, but not long filiform and flexuous	Mature photosynthetic leaf blades bluish, soft, rolling immediately on detachment from sheaths, apices long filiform and flexuous
Distal leaves of actively growing sterile shoots with fine, white, erect hairs behind ligule (usually shorter and fewer than in *P. australis*, occasionally lacking)	Distal leaves of actively growing sterile shoots with long, coarse, white, erect hairs behind ligule
Sheath mouth with dense tufts of short white trichomes	Sheath mouth hairy, but without dense tufts of short, white trichomes
Lower leaves of aerial stems deciduous: each blade and sheath falling together leaving internode naked and axillary bud exposed	Blades only, of leaves of aerial stems, deciduous: each sheath persistent, investing internode and axillary bud
Abscission zone developed at base of leaf sheath	Abscission zone developed at base of leaf blade
Axillary buds hardly recessed into stem tissue, oval, without basal pediment	Axillary buds recessed into stem tissue, round, with basal pediment
Mature aerial stems with few to many expanded axillary shoots	Mature aerial stems usually without expanded axillary shoots
Apices of leaves to axillary shoots pungent	Apices of leaves to axillary shoots soft, never pungent (firm to hard, but not penetrating under brackish or xeric habitat conditions)
Inflorescences lax, with strongly drooping branches: usually more than 6 leaves persisting below each inflorescence, not lying in a single plane, uppermost not sheathing inflorescence base	Inflorescences compact, with slightly drooping branches: 6 or fewer leaves persisting below, often lying in a single plane, uppermost usually sheathing inflorescence base
Stems bearing old inflorescences dying back distally only: otherwise remaining photosynthetic	Stems bearing old inflorescences dying back to ground level
Spikelets of 3—7 (4, 5) florets	Spikelets of 3—9 (5, 6) florets
Upper glume 3·0—5·7 (mode 4·0) mm long	Upper glume 5·0—9·2 (mode 7·0) mm long
Sum of lengths of lower and upper glume and first lemma 10·2—19·7 mm	Sum of lengths of lower and upper glume and first lemma 18·3—27·0 mm
Abaxial epidermis of leaf blade with outgrowths from epidermal cells in form of: (1) prickle hairs, scattered over the veins in particular, (2) micro-hairs, thinly scattered between the stomatal bands and the veins	Abaxial epidermis of leaf blade with outgrowths from epidermal cells in form of: (1) unpointed prickles over the veins (no prickle hairs seen), (2) hooks (as distinct from prickle hairs) between the veins, most frequent amongst the stomata, each hook usually paired with a cork cell (microhairs never observed)

Citation of Material Studied

Both species have been adequately described by other authors, so it is not considered necessary to re-describe them here, especially as significant features by which they may be distinguished have been emphasized in the keys provided and in the summary of differences. Populations studied in detail are listed in tables 1 and 2, together with a brief résumé of habitat conditions in each case. Other populations studied in the field and from which herbarium specimens were obtained are listed below. Complete sets of all numbers prepared during the present work are deposited in the herbaria of the University of Natal, Pietermaritzburg, and University College, Durban (population samples: University of Natal only).

The additional herbarium specimens studied are not cited, as the material consisted, with few exceptions, of the distal tips of flowering stems. However, to give some guide to the distribution of each species in southern Africa as this is known at present (excluding Natal for which province distribution maps are provided: figs. 18a, b), countries or provinces, and where possible magisterial districts, from which specimens have been seen and could thus be identified with one or other taxon according to the criteria of difference presented here, are also listed.

Phragmites mauritianus Kunth, Rev. Gram. I: 277 (1830); Hubb. in Hill, Fl. Trop. Afr. X, I: 155 (1937); Chippindall, Grasses and Pastures of S. Afr.: 229 (1955); Clayton, Kew Bull. 21, 1: 117 (1967).

Other populations studied in the field

2930 (Pietermaritzburg) Pietermaritzburg (-CB), banks of Umsindusi River. *Gordon-Gray 6153;* Durban Bluff (-DD), on flats on road to Wentworth Hospital. *Gordon-Gray 6156A;* Isipingo North (-DD), 29°59′S, 30°57′E *Ward 6580;* Isipingo North (-DD), 29°59′S, 30°57′E *Ward 6591;* Isipingo Flats (east) (-DD), 29°59′S, 30°57′E former course of Mlazi River *Ward 6552;* 3030 (Port Shepstone) Mpenjathi River (-CD) 30°58′S, 31°16′E main S. Coast road bridge *Ward, 6757.*

Localities verified

Angola: South West Africa (Amboland): Transvaal (Pietersburg, Waterval Boven and Nelspruit distrs.): Swaziland (Pigg's Peak, Mbabane and Hlatikulu distrs.).

Phragmites australis (Cav.) Trin. ex Steud., Nom. Bot. ed. 3, 2:324 (1841); Clayton, Taxon 17, 2:168 (1968).

P. communis Trin., Fund. Agrost.: 134 (1820); Stapf, in Thiselt.-Dyer Fl. Cap. 7:541 (1898); Hubb. in Hill, Fl. Trop. Afr. X, 1:153 (1937); Chippindall, Grasses & Pastures of S. Afr.: 228 (1955); Clayton, Kew Bull. 21, 1:116 (1967).

Other populations studied in the field

2929 (Underberg) Tabamhlope Research Station (-BA) in stream *Gordon-Gray 6281;* Mooi River (-BB) north bank of river in the town *Gordon-Gray 6280;* 2930 (Pietermaritzburg) Umgeni River, Midmar Dam (-CA) downstream of main dam wall *Gordon-Gray 6160A;* Wentworth (-DD) swamp near S.A.R. station 29°54′S, 30°49′ E *Ward, 6578;* Isipingo Beach (-DD) 29°59′S, 30°56′E *Ward, 6583;* ditto *Ward 6594; 6595; 6764; 6763;*

2930 (Pietermaritzburg) Isipingo River (-DD) 29°59′S, 30°56′E *Ward, 6598;* Isipingo Flats (east: former course of Mlazi River 29°59′S, 30°57′E *Ward, 6550; Ward 6551;* 2930 (Pietermaritzburg) Isipingo North 29°58′S, 30°57′E *Ward, 6592;* Isipingo North 29°59′S, 30°57′E *Ward, 6585.*

Localities verified

South West Africa (near Namutoni; near Grootfontein; near Swakopmund; near Windhoek): Orange Free State (Bloemfontein distr.): Lesotho (Leribe distr.): Cape Province (Umzimkulu, Mount Currie, Umtata, Idutywa, Kentani, Komgha, Kingwilliamstown, Albany, Port Elizabeth, Humansdorp, Middelburg, Uitenhage, Joubertina, Knysna, George, Uniondale, Oudtshoorn, Riversdale, Swellendam, Stellenbosch, Worcester, Simonstown, Malmesbury, Clanwilliam, Herbert and Barclay West distrs.).

Subsequent field work by one author, CJW, has revealed the presence of *P. mauritianus* at several localities in the Transkei, the southernmost being the Bashee Bridge where the main Transkei-Cape road crosses the Bashee river.

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TANNINIFEROUS IDIOBLASTS IN THE MESEMBRYANTHEMACEAE

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Abstract

The leaves of most *Mesembryanthemaceae*, when preserved, dehydrated, and cleared, display a pattern of tanniniferous idioblasts. A technique for processing the leaves is presented and questions are raised concerning the adaptive value of these cells and the possible use of their location-patterns as a diagnostic feature in taxonomy.

Uittreksel

TANNIENHOUDENDE IDIOBLASTE IN MESEMBRYANTHEMACEAE. Die blare van meeste Mesembryanthemaceae, nadat dit gepreserveer, ontwater en verhelder is, vertoon patrone van tannienhoudende idioblaste. 'n Tegniek om die blare voor te berei word aangebied en die vraag wat die aanpassingswaarde van gebruik van hulle plasingspatroon as 'n diagnostiese kenmerk taksonomie bespreek.

Introduction

The most arresting feature of a preserved, dehydrated, and cleared leaf of almost all of those desert succulents commonly named "mesembs" is the large number of tanniniferous idioblasts that are visible. My own first encounter with these cells came during my study of the internal structure of *Lithops* and they were noted in the two papers that resulted (Dugdale, 1966, 1968). An extension of that study to the leaves of other mesembs discloses that tanniniferous idioblasts are of very common occurrence in this group of plants. Indeed, it might very well be true that a fuller understanding of these cells could lead to a better understanding of the evolutionary relationships within the group. With the hope, then, of stimulating the interest of students of succulent plants in the study of tanniniferous idioblasts, the following formula and techniques are presented.

Materials and Methods

Remove several leaves from a plant and with a razor blade cut some transversally into sections 4–5 mm thick and split others in half longitudinally. If the leaves are sufficiently wide, it is advantageous to split them into thirds rather that into halves. The pieces of leaves are placed into suitably-sized glass jars by species and an identifying label, written in pencil on a piece of index card, is inserted in each jar. This label will be legible when the processing is completed.

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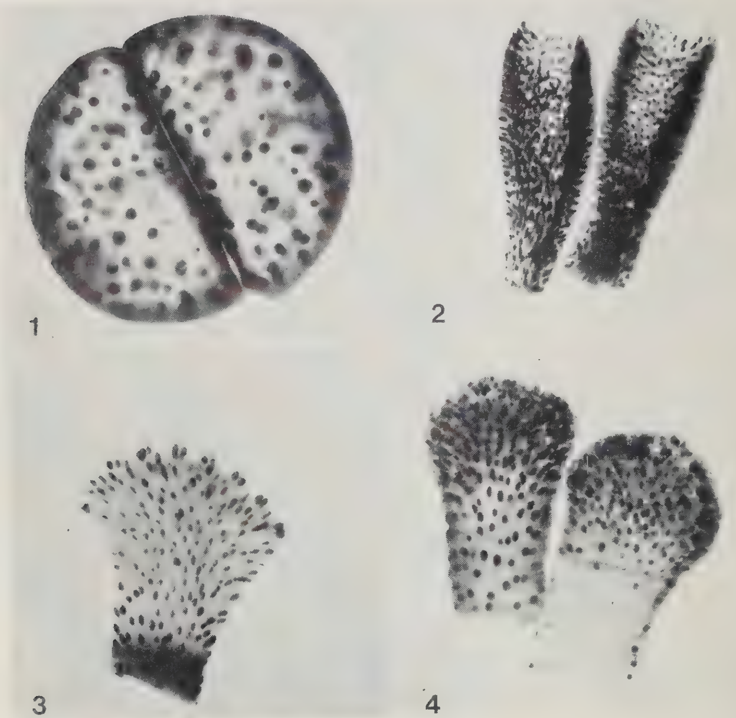

FIG. 1–4.
Fig. 1. *Lithops menellii.* Fig. 2. *Fenestraria aurentiaca*, two halves of same leaf. Fig. 3. *Titanopsis malherbii.* Fig. 4. *Titanopsis calcarea*, front and back of same leaf.

A satisfactory solution for fixing succulent plant tissue follows.

Phosphomolybdic acid	0·8	gm.
Glacial acetic acid	5	ml.
40% Formalin	5	ml.
Water	90	ml.

Pour this solution over the leaf sections in each jar and let them soak for 24 hours. Pour off the fixing solution and replace, at 24 hour intervals, with 80, 95, and two changes of 100% ethyl alcohol. If different batches of material are being processed over a period of time, the used absolute alcohol can be re-used in the lower percentages, since only the 100% alcohol is critical. After

dehydration is complete, replace the absolute alcohol with xylol. (If any cloudiness is apparent, immediately replace the xylol with absolute alcohol for another 24 hours.) After 24 hours in xylol the tissue should be completely cleared and the tanniniferous idioblasts will appear as dark mahogany to black-coloured bodies.

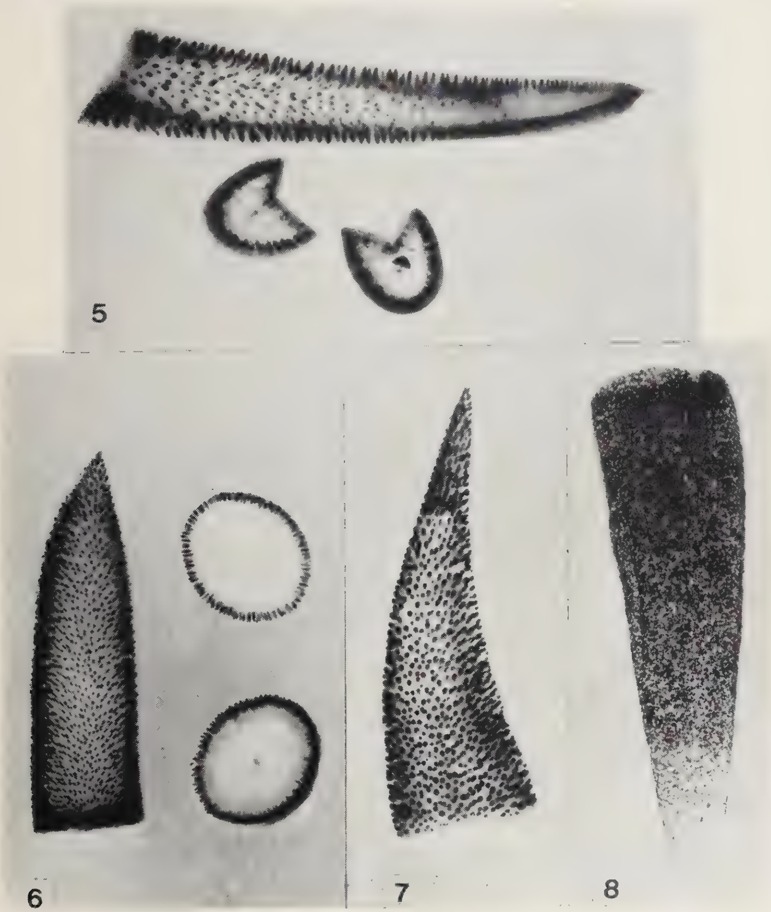

FIG. 5–8.
Fig. 5. *Cheiridopsis candidissima.* Fig. 6. *Cylindrophyllum calamiforme.* Fig. 7. *Bergeranthus vespertinus.* Fig. 8. *Adromischus festivus* (Crassulaceae).

The preserved leaves can be photographed while under xylol in a deep watch glass by transmitted light. Single lens reflex cameras with a macrolens and behind-the-lens metering are particularly appropriate for this work.

Discussion

On the basis of having processed hundreds of plants it can be said that tanniniferous idioblasts occur in varying quantities and patterns in all species of *Lithops*. However, in, for instance, *L. hallii* and *L. salicola* they are restricted to the sepals of the flower and do not appear, except perhaps occasionally, in the main body (leaves) of the plant. In those species of *Lithops* in which these cells are present within the leaves, they appear to occur in fairly distinctive and constant patterns. On occasion I have been able to identify the species of a preserved *Lithops*, in which all other clues are obliterated, solely upon the basis of its idioblast pattern. Even more often one is able to say that a given preserved plant could not be of a certain species because its idioblast pattern is not correct. It is my belief that it will be possible someday to produce a key to the *Lithops* species based upon these patterns used in conjunction with the external diagnostic features.

Outside of the genus *Lithops*, moreover, tanniniferous idioblasts are widely, and perhaps universally, found among the other mesembs. I have recently processed leaves from more than 25 species within 15 genera and idioblasts occurred in almost all of them. Three exceptions were: *Nananthus aloides*, *Gibbaeum petrense*, (but in *G. album* they are present as very fine granules) and *Glottiphyllum parvifolium*. *Delospermum echinatus*, whose affinities have been questioned by others, also had no idioblasts. As in *Lithops*, however, the possibility remains that the idioblasts in these species may occur only in the sepals of the flowers which were not available to me at the time. It is also interesting to note that the leaves of some 5 or 6 *Adromischus* species which were tested were so densely populated with idioblast cells as to be uniquely distinctive.

Conclusion

Tanniniferous idioblasts are of interest from two points of view. First of all there is the purely morphological problem of discovering and recording their presence or absence in the various species and of determining whether or not their patterns of dispersal within the leaf are constant and distinctive enough to serve as a taxonomic aid. Secondly, there is the problem of their adaptive value. Several possibilities come to mind: as a source of chemicals used in the healing process, as a deterrent to being eaten by animals, or as a light shield against certain/all wavelengths of light. On a purely speculative basis, I prefer this third possibility, but the answer would need to be experimentally determined.

ACKNOWLEDGMENTS

The author is grateful to Mr. Ronald Majka for his assistance in processing the leaves and to the National Botanic Gardens of South Africa, Kirstenbosch, for supplying a large assortment of correctly identified leaves for our use.

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ALOE BUHRII: A NEW SPECIES FROM THE CALVINIA DISTRICT, CAPE PROVINCE

J. J. Lavranos

ABSTRACT

A new species of Aloe from the Calvinia district of the Cape Province is described. It is considered to be related to *A. striata* Haw.

UITTREKSEL

'n Nuwe Aloe-soort uit die Calviniadistrik in die Kaapprovinsie word beskryf. Dit word geag verwant te wees aan *A. striata* Haw.

Aloe buhrii Lavranos nov. sp., affinis *A. striatae* Haw., sed ab ea foliis arcuatis, erectis, marginibus minute denticulatis, inflorescentiis laxe paniculatis, stigmate post anthesin a 5 mm exserto satis differt.

Plantae acaules; *foliis* lanceolatis, deltoideis, arcuatis, erectis, vel adscentibus, a 40 cm longis, 9 cm latis, carnosis supra planis sed apicem versus leviter canaliculatis, subtus convexis, utrinque glaucis, irregulariter maculis albescentibus, elongatis, nonnunquam confluentibus obtectis; marginibus cartilagineis, rubidis, dentibus minutissimis, osolescentibus; *inflorescentiis* laxe paniculate, a 60 cm altae, 7-15-ramosa, pedunculo valido, basi 12—15 mm lato; *racemis* sub-capitatis, aliquantum laxis, floribus aurantiacis; *bracteis* deltoideis, acutis, 5—10 mm longis; *pedicellis* 20—25 mm longis; *perigoniis* 25—27 mm longis, basi inflatis et 6 mm diam., supra ovarium a 4 mm constrictis, deinde decurvulis, orem versus paulo dilatatis, segmentibus exterioribus per 6—7 mm liberis; *filamentis* valde applanatis, tractu temporis a 3 mm exsertis; *stigma* post anthesin a 5—6 mm exsertum; *ovarium* viridulum, 5 mm longum, 2 mm latum.

Type Locality: South Africa: Cape Province;—3119 (Calvinia). Isolated hills, 6 km E of the Bokkeveld Plateau, (-AA) alt. appr. 650 m, *Buhr in Lavranos 8163* (PRE holotype).

Plants stemless dividing into several heads, the rosettes usually upright; *leaves* about 16, lanceolate-deltoid, arcuate-erect or ascending, 40 cm long, 9 cm broad at base, fleshy, rather soft, their upper surface flat but slightly canaliculate towards the apex, glaucous, reddish tinged, distinctly striate and covered irregularly but in parts densely with pale, elongate or "H"-shaped and often confluent

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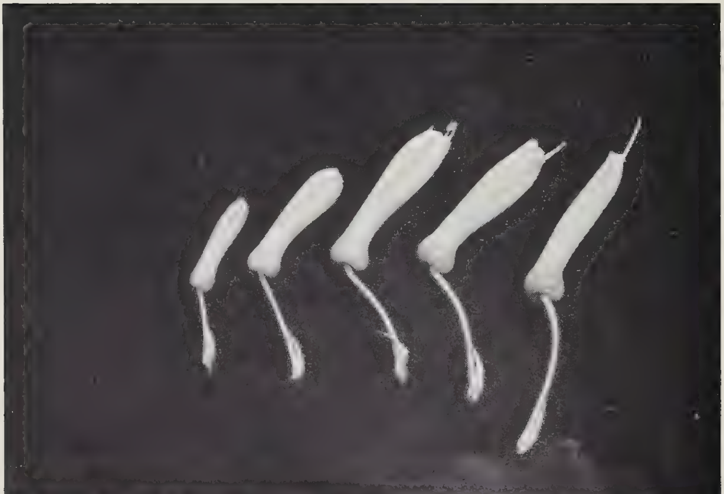
Plant flowering at Zwartkops, Transvaal.

Detail of the inflorescence



Flowers, natural size.

Fig. 1. *Aloe buhrii* Lavranos.

Photos: H. Bornman

spots; their lower surface convex, otherwise as the upper; the margins with a pale red, cartilaginous, denticulate or sub-entire border, 1,5—2,0 mm wide, the denticles obtuse, less than 1 mm long, usually 3,5 mm distant but often laterally confluent; *inflorescence* laxely paniculate, to 60 cm tall, branching above the middle into 7—15 rather short lateral branches, the lower ones rebranched, each branch or branchlet subtended by a broadly deltoid, yellowish, 5-8-nerved bract; *peduncle* basally biconvex, becoming sub-terete upward, rigid, 12—18 mm broad near its base; *racemes* sub-capitate, rather laxely flowered, the buds green tipped, the flowers orange-red, pendulous at the end of horizontally spreading *pedicels* which are the same colour as the perianths; *floral bracts* very narrowly deltoid, acute, 5—10 mm long, yellowish, 3-5-nerved; *perianths* 25—27 mm long, with a basal swelling 6 mm diam., constricted to 4 mm above the ovary, thence slightly decurved and widening toward the mouth, their outer segments free for 6—7 mm, with 3 congested and apically confluent orange-red nerves, the inner segments broader than the outer; *stamens* with yellow, filiform and much flattened filaments, the anthers in turn exserted by 3 mm; *style* yellow, its stigma at length exserted by 5—6 mm; *ovary* pale green, 5 mm long, 2 mm broad.

A. buhrii has escaped discovery, and perhaps annihilation, because of its seemingly very limited range in an area which is both remote and not directly accessible by road. It is restricted to a few isolated hill tops standing in advance of the Eastern side of the Bokkeveld Plateau, above the Swart Doorns River gorge, where it grows in karroid veld on shales of the Malmesbury system. The average annual rainfall on this side of the Bokkeveld is of the order of 150—200 m and is confined almost exclusively to the winter months, May to September. The climate is mild in winter with only light frosts, but hot in summer.

Despite its very different appearance, *A. buhrii* is related to *A. striata* and its associates with which it has in common striate leaves with broad, cartilaginous, red margins bearing obsolescent teeth, much branched inflorescences with rather capitate racemes, long pedicels and flowers with a basal swelling and outer segments free for only 6—7 mm. It divides into several rosettes but does not produce suckers.

The new species differs from its relatives by its arcuate-erect or steeply ascending leaves with their denticulate margins, its paniculate (not corymbose) inflorescences, which are much less branched than in *A. karasbergensis* Pillans and the fact that the style becomes exserted by 5 mm or more after anthesis.

The specimen here figured may not be wholly typical where the inflorescence is concerned, as it flowered out of the soil and some of the lateral racemes aborted in consequence.

FIG. 2. *A. buhrii.* Typical group of plants in habitat.
Photo: J. J. Lavranos

When I first examined these plants and noticed their affinities with the *striata* group of Aloes, I investigated the possibility that they might be of hybrid origin, one of the parents being *A. striata* or *A. karasbergensis*. However, neither of these species is found within a radius of some 250 km of the Bokkeveld. *A. melanacantha* Berger and *A. glauca* Mill. are the only two species which grow in close proximity to the new species while *A. mitriformis* Mill., *A. krapohliana* Marl., *A. khamiesensis* Pillans and *A. dichotoma* Masson occur on or near the Bokkeveld as does *A. falcata* Baker. None of these species is in any sense related to *A. buhrii*.

The species is named after Mr. Elias A. Buhr, of Nieuwoudtville, in the Western Cape Province, who recognised it as new to science and is a keen student and nature conservationist. I am indebted to him for the plants on which this description is based and for most of the information about them. I must thank Mr. Dubois, of Pretoria for conveying to me a plant in bud, a rather delicate operation; also Mr. Bornman for the photographs accompanying this text.

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TWO NEW SPECIES OF ALOE (LILIACEAE) FROM TROPICAL AFRICA

L. C. Leach

ABSTRACT

Two new species of *Aloe* (*Liliaceae*) are described, their apparent relationships discussed and their positions in the "Key to the species" in Reynolds, The Aloes of Tropical Africa and Madagascar (1966), are indicated.

UITTREKSEL

TWEE NUWE ALOE-SOORTE (LILIACEAE) VAN TROPIESE AFRIKA. Twee nuwe *Aloe-soorte* (*Liliaceae*) word beskryf, hulle blykbare verwantskap bespreek en hul plek in die „Sleutel tot die soorte" in Reynolds, *The Aloes of Tropical Africa and Madagascar* (1966) word aangedui.

Aloe cannellii Leach, sp. nov.

A. wildii (Reynolds) Reynolds affinis sed planta parviore magis caespitosa; foliis angustioribus rosulatis, marginibus cartilagineis angustis hyalinis (in sicco albescentibus), dentibus parvioribus confertioribus; floribus brevioribus minus ventricosis; capsulis parvioribus differt.

Planta caespitosa, habitu patulo vel pendenti, surculis quaquaversus effusis ex caulorhiza substuberosa exilientibus; radices carnosae subfusiformes. *Folia* plerumque 4—5, rosulata, ad 26 cm longa, 4—8 mm lata, linearia, basaliter dilato-amplexicaulia, in apicem acutum gradatim angustata, patula vel flaccida, e brunneo viridia; marginibus angustis cartilagineis hyalinis (in sicco albescentibus), dentibus acutis minutis, c. 0·25 mm longis, plerumque c. 1 mm distantibus. *Inflorescentia* simplex, 20—30 cm alta, erecta vel ascendenti-erecta. *Pedunculus* gracilis, teres (infra interdum leviter compressus), c. 3 mm diam., viridis; bracteis sterilibus 5—6, quam bracteis floralibus multo grandioribus. *Racemus* floribus 14—15 (10—20) laxe dispositis, c. 10 cm longus (12·5); gemmis initio suberectis mox patentissimis, atrocarmineis ad apicem caesio-viridibus mox viridescentibus; floribus apertis subpendulis, coccineo-auriantiacis ad apicem viridibus. *Bracteae* scariosae, exalbidae, ovato-acutae, 4·5—6·5 mm longae, 3—3·5 mm latae; nervis 3, obscuris, confluentibus, rubro-brunneis. *Pedicelli* 10—13 mm longi, perianthio basi stipitatae articulati. *Perianthium* coccineo-auriantiacum ad orem viridescens, cylindraceo-trigonum, basaliter subobconicum breviter stipitatum, supra medium subventricosum, 20—22 (25) mm longum, prope basin c. 3·5—4 mm diam., inde ad c. 5 mm amplificatum, tum ad c. 4 mm prope orem patulum constrictum; *segmenta exteriora* basi libera,

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nervis obscuris 3, ad apicem confluentibus viridibus; *segmenta interiora* quam exteriora latiora et obtusiora, marginibus tenuis exalbidis translucidis, nervis obscuris 3, perleviter auriantico-carinata, ad spicem viridula. *Antherae* inclusae. *Stigma* demum vix vel haud exsertum. *Ovarium* viridulum vel lutescens, c. 4·5 mm longum, 1·75—2 mm diam. *Capsula* (sicca) bubalina, longitudinaliter caperata, 11·5 mm longa, c. 4·5 mm diam.; lobis non valde patulis, medio valde sulcatis. *Semina* atro-brunnea, parce minute pusticulato-tuberculata, superficiebus imparibus perleviter convexis 4—5, angulis parum alatis, c. 3·5 mm longa.

Type: Moçambique, Manica e Sofala Distr., *I. C. Cannell* 33 (LISC; PRE; SRGH, holo.).

Moçambique. **MS**: Manica e Sofala Distr., cult. Bulawayo, Rhodesia, fl. Aug. 1968, *I. C. Cannell* 33 (LISC; PRE; SRGH), idem Hort. *Bullock*, Bulawayo, fl. March 1967 (LMA), ibid. cult. Greendale, fl. 25.iv.1970, *Leach & Cannell* 14407 (K).

Fig. 1.
Cultivated plant flowering at Bulawayo, Aug. 1968.
I. C. Cannell 33.

FIG. 2.
Subtuberous rootstock with fleshy subfusiform roots.
Leach and Cannell 14407.
Aloe cannellii Leach.

The flowering period of this species appears to be very variable; plants in cultivation flower almost continuously if watered (cf. *A. ballii* Reynolds).

A. cannellii appears to be most closely related to *A. wildii* which is endemic to the Chimanimani Mountains, and with which it possibly forms a vicariant pair. The new species differs from this its nearest relative in being a smaller, more tufted plant with narrower rosulate leaves with narrow hyaline cartilaginous margins and smaller more closely set teeth; the smaller flowers are less markedly ventricose and the darker coloured seeds are contained in a much smaller capsule. In leaf characters only, the new species is possibly nearer to *A. torrei* Christian et Verdoorn but differs therefrom in many other ways.

The seeds of *A. inyangensis* Christian, *A. howmanii* Reynolds, *A. hazeliana* Reynolds, *A. musapana* Reynolds, *A. wildii* and *A. cannellii* are all somewhat similar as to size and shape, but are distinguishable from each other by their colour, which appears, from the admittedly limited material available, to be constant for a given species.

A. cannellii is named in honour of Mr. Ian Cannell who, in the course of numerous botanising excursions in the Flora Zambesiaca area, has made several interesting discoveries, including the attractive new species now described. Plants were found not far from the summit of an isolated mountain in the Manica e Sofala District of Moçambique; the exact locality is not herein disclosed as it is feared that consequent depredations by "collectors" might eliminate the species from its natural habitat, which is, as far as is known, restricted to one relatively small area.

Plants are not very plentiful and appear to occur only on south-east facing, almost vertical cliffs, at an altitude of $\pm$ 1500 m. Embedded in peat-like masses of grass tufts and roots, plants are by no means conspicuous and but for an out of season inflorescence would possibly have remained undiscovered. Although the flowering of this solitary specimen was almost over it was recognised by Mr. Cannell as being different from any of the related species known to him and after some diligent searching, further rather dried up plants were found. Two or three of these were collected and placed in cultivation at Bulawayo, where they subsequently flowered, enabling photographs to be taken, material prepared and a description drawn up.

This addition to Berger's Section *Leptoaloe* would fit into Reynolds's key in "Aloes of Tropical Africa and Madagascar: 11 (1966)" under Group 3 "Leaves always rosulate": "B Plants acaulescent or almost so" and is distinguished from the others in the group by its much shorter (10—15 mm) pedicels and shorter (20—25 mm) perianth.

Plant tufted, with shoots spreading in all directions, arising from a partially exposed subtuberous rootstock with fleshy subfusiform roots; plants forming clumps with a spreading or pendent habit. *Leaves* green or with a brownish tinge, rosulate, usually 4—5, up to 26 cm long, 4—8 mm wide, linear, basally dilated-amplexicaul, gradually tapering into the acute apex, spreading to flaccidly decurved, with a narrow hyaline (drying whitish) cartilaginous margin armed with minute, translucent, whitish, acute teeth about 0·25 mm long and rather variably spaced, generally $\pm$ 1 mm apart (occasionally a leaf may be found in which both margin and teeth are partially absent); *upper surface* more or less flat below, shallowly canaliculate above, sometimes with a few scattered whitish spots in the lower portion, *lower surface* convex, more copiously white spotted from about half way, the spots becoming more crowded towards the base. *Inflorescence* simple, 20—30 cm tall, erect or ascending-erect. *Peduncle* slender, terete (sometimes slightly compressed below), c. 3 mm diam., green, devoid of bloom, with 5—6 sterile bracts which are much larger than the floral bracts. *Raceme* laxly 14—15 flowered (10—20), about 10 cm long (12·5); buds at first suberect soon becoming widely spreading, dark carmine blue-green tipped,

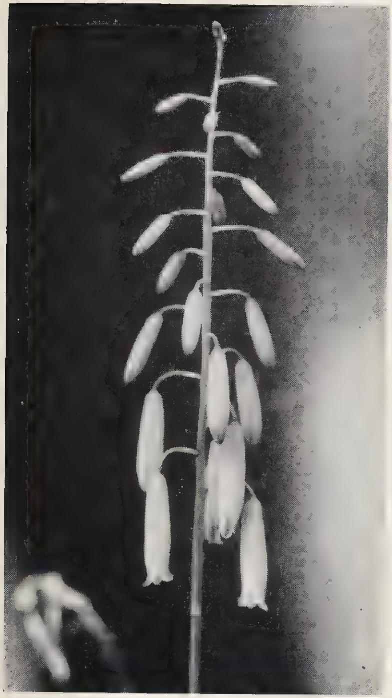


Fig. 3.

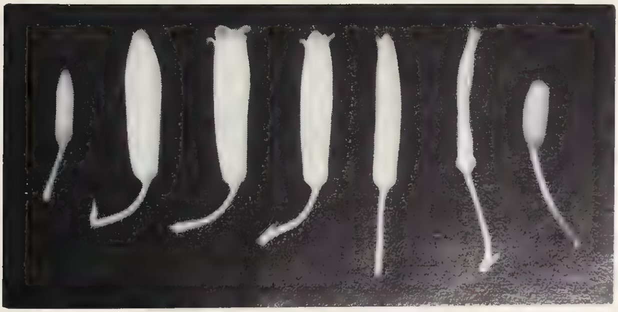
An exceptionally long raceme, shewing flowers with the perianth sharply constricted just below the widely open mouth. Clone of *Cannell* 33 cult. Salisbury, *N. D. Bey*.

Photo by courtesy of Mr. N. D. Bey.

Fig. 4.

Flowers 1/1, bud to young capsule from the above raceme *Aloe cannellii* Leach.

Photo L. C. Leach.



soon becoming paler with greenish tip; open flowers subpendulous, red-orange, green tipped. *Bracts* scarious, whitish with 3 indistinct, confluent red-brown nerves, ovate acute, 4·5—6·5 mm long, 3—3·5 mm wide. *Pedicels* 10—13 (15) mm long, articulated to the stipitate base of the perianth. *Perianth* orange-scarlet grading into orange towards the greenish mouth, cylindric trigonous, basally subobconic, shortly stipitate, slightly ventricose above the middle, 20—22 (25) mm long, about 3·5—4 mm diam. towards the base, enlarging to ± 5 mm, then again slightly, although somewhat sharply, constricted to about 4 mm diam. immediately below the widely spreading apices of the segments; *outer segments* free to the base, orange-scarlet to orange with three obscure nerves becoming bright green at their confluent apex; *inner segments* free, wider and more obtuse than the outer, with thin, translucent, whitish margins and three obscure nerves forming a slight keel, orange towards the base becoming bright green at the apex. *Filaments* pale translucent green to white, the three inner lengthening before the outer; *anthers* not exserted, red-orange with peach coloured pollen; *style* whitish at the base becoming pale yellowish green towards the transclucent whitish stigma, which is not or scarcely exserted. *Ovary* 6-grooved, yellow-green to orange-yellow, c. 4·5 mm long, 1·75—2 mm diam. *Capsule* (dry) brownish buff, longitudinally wrinkled, 11·5 mm long, ± 4·5 mm diam.; lobes not widely spreading, each with a deep median furrow. *Seeds* dark brown, sparingly minutely pusticulate-tuberculate, with 4—5 unequal, slightly convex faces, winged on the angles but not very prominently so, ± 3·5 mm long × 1·25 mm diam.

Aloe trigonantha Leach, sp. nov.

A. crassipedi Bak. affinis sed plantis surculis basilaribus aggregatis; foliorum dentibus parvioribus; racemis laxioribus floriferis, floribus scarlatinus, segmentis ad apicem minutissime denticulatis; bracteis parvioribus attenuatioribus, prominenter medinervibus saepe uninervibus, margine minutissime denticulato distinguenda.

Plantae acaulescentes, e basi surculis aggregatis. *Folia* c. 24, dense rosulata, valde patentia, 30—45 cm longa, basi 5—10 cm lata, apicem versus leviter recurva vel aliquantum flaccida, plerumque parte apicali siccata marcidaque; *supra* pallide viridia sparsim albo-maculata, spicem versus roseo-brunnescentia, basi leviter concava, superne aliquantum canaliculata; *subtus* convexa, pallide caesio-viridia modice albo-maculata; *margines* dentibus pungentibus deltatis vel interdum uncinatis, ± 3 mm longis, 1—2 cm distantibus armati. *Inflorescentia* paniculata, infra medium ramosa, 60—90 cm alta. *Pedunculus* viridis (in sicco brunneus), basi plano-convexus, usque ad 2 cm latus. *Racemi* laxe floriferi, cylindraceo-acuminati, c. 20 cm longi, 7 cm diam., gemmis patulis et floribus apertis cernuis. *Bracteae* deltato-attenuatae vel ovato-acuminatae, scariosae,

brunneo-albae, 5—10 mm longae, 3—5 mm latae, prominenter medinerves saepe uninerves, marginibus minutissime denticulatis. *Pedicelli* patuli, usque ad 15 mm longi. *Perianthium* scarlatinum, crassum carnosumque, breviter stipitatum, 35 mm longum, ad basim subtruncatum 10—12 mm diam. inde gradatim decrescens, sigillatim trigonum, 7—8 mm diam. leviter lateraliter compressum, ad orem apertura triangulari 3—4 mm lata; *segmenta* ad apicem acuta, minutissime denticulata; *exteriora* per 10 mm libera, obscure triplinervia; *interiora* latiora, carinata, apice patulo-recurva. *Antherae* inclusae vel perbreviter exsertae. *Ovarium* viride, 6·5 mm longum, c. 3 mm diam. *Stylus* demum vix vel usque ad 1 mm exsertus. *Semina* atro-brunnea, tenui-alata, irregulariter et variabiliter triquetra, 5·5—7 mm longa, c. 3 mm lata.

Type: N. Ethiopia, Begemdir Province, *MacLeay* in *Reynolds* 11618 (PRE, holo.; SRGH).

Ethiopia: Begemdir Prov., between Gondar and Lake Tana, alt. ± 2500 m, cult. Mbabane, Swaziland, fl. 15.viii.1965, *MacLeay* in *Reynolds* 11618 (PRE, holo.; SRGH), idem Hort. *A. J. Jones*, White River, Transvaal, fl. 27.vii.1966, (BR; MO), idem Hort. *Leach*, Nelspruit, Transvaal, fl. 9.vii.1967 (EA; K).

Aloe trigonantha was discovered by Professor K.N.G. MacLeay, at that time of the Department of Botany, University College of Khartoum, who found plants "common in grass near the roadside, between Gondar and Lake Tana, at an altitude of approximately 2500 m." Lake Tana lies athwart the boundary between the Begemdir and Gojjam Provinces of N. Ethiopia at an altitude of 1830 m, at approximately 12° 00′ N: 37° 30′ E.

Live plants sent to the late Dr. Reynolds flowered in cultivation at Mbabane, Swaziland, for the first time on 15th August 1965 at a time when Dr. Reynolds's health was beginning to fail and the manuscript for his second exhaustive monograph was demanding all his energies. Despite this preoccupation however, photographs were taken, herbarium material prepared and a partial description drawn up. Plants of clonal origin subsequently flowered in Dr. A. J. Jones's garden at White River, Transvaal and in the author's garden at Nelspruit, when further specimens were obtained, enabling the description eventually to be completed and relationships assessed.

The new species appears to be most closely related to *A. crassipes* Bak. but differs in forming groups from basal shoots, in having more widely spreading more softly textured, less fiercely armed leaves (which are even closer to those of *A. christianii* Reynolds than are those of *A. crassipes*), and laxly flowered racemes of scarlet flowers with the acute apices of their perianth segments minutely denticulate; the smaller, more attenuate, plicate-keeled bracts with minutely denticulate margins and a prominent, often solitary median nerve are

Fig. 5.
Cultivated plant flowering at Mbabane, Swaziland. Height 90 cm. *Reynolds* 11618.
Aloe trigonantha Leach.
Photo by courtesy of the late Dr. G. W. Reynolds.

also quite different from those of *A. crassipes* which are somewhat fleshy, not at all keeled, and have 4—5 $\pm$ equal, not at all prominent nerves and entire margins.

There appears also to be an affinity with *A. percrassa* Tod. and particularly with *A. steudneri* Schweinf., which both occur in the same general geographical region and appear to occupy somewhat similar montane habitats. However,

A. trigonantha differs in several respects from both of these in having widely spreading leaves, a more freely branched panicle of more laxly flowered racemes, perianth segment apices minutely denticulate, and bracts with a prominent often solitary median nerve and minutely denticulate margins. From the former the new species is also immediately distinguished by its much larger fleshy flowers, and from the latter in having smaller flowers with segments which are free for only 10 mm (those of *A. steudneri* are 40—45 mm long with segments free almost to the base) and much smaller bracts.

The flowers of the new species are exceptionally fleshy and markedly triangular in cross-section. It should perhaps be mentioned that the flowers, possibly due to their fleshiness, appear to shrink considerably when dried (those recorded by Reynolds as 35 mm long, measure only $\pm$ 28 mm in the dried material, similar shrinkage was observed in material prepared by the author).

FIGS. 6 and 7.

Cultivated clone of *Reynolds* 11618 flowering at Nelspruit, height 60 cm.

Flowers 1/1, from bud to post pollination stage.

Aloe trigonantha Leach.

Photos L. C. Leach.

A. trigonantha appears to be morphologically so close to *A. crassipes* and also, although to a somewhat lesser extent, to *A. christianii* and *A. pretoriensis* Pole Evans that it seems logical that it should be included in Reynolds's Group 12 (Reynolds, Aloes Trop. Afr. & Madag. 1966). Its inclusion here does however, require some slight modification to the diagnosis of that Group, inasmuch as the leaves of the new species are obscurely white spotted and its perianth averages 35 mm in length. Subject to these adjustments *A. trigonantha* would then "key out" under:—

GROUP 12

A small to medium sized plants with a branched *inflorescence* up to 1 m high; *pedicels* 14—15 mm long.

(1) *Plants* solitary; *leaves* unspotted; *inflorescence* 50—60 cm high; *bracts* 10 mm long; *perianth* 38 mm long, dull yellowish green . . . . *A. crassipes*

(1a) *Plants* forming groups from basal shoots: *leaves* obscurely white-spotted; *inflorescence* 60—90 cm high; *bracts* 5—10 mm long with a prominent median nerve; *perianth* 35 mm long, scarlet. . *A. trigonantha*

Plants acaulescent, forming dense groups from basal shoots. *Leaves* about 24, densely rosulate, widely spreading, slightly recurved or somewhat flaccid towards the apex, usually with the apical portion dry and withered, 30—45 cm long, 5—10 cm broad at the base; *upper surface* pale green with a few elongated whitish markings, becoming pinkish brown towards the apex, sometimes with a purplish tinge towards the margins, shallowly concave low down becoming somewhat canaliculate above; *lower surface* rounded, pale blueish green, more copiously white-spotted than the upper; *margins* narrow, pinkish brown, cartilaginous, armed with deltate or sometimes uncinate teeth $\pm$ 3 mm long, 1—2 cm apart low down, more widely spaced above, with the interspaces straight or occasionally slightly curved. *Inflorescence* a branched panicle, branched well below the middle, 60—90 cm high with $\pm$ 3 main branches each bearing up to 4 secondary branches, all with a pair of broad scarious whitish bracts at their base. *Peduncle* plano-convex below, up to 2 cm wide towards the base, green with a very faint bloom (peduncle and branches brown when dry). *Racemes* rather laxly flowered, cylindric-acuminate, $\pm$ 20 cm long, 7 cm diam., with the buds spreading and the open flowers cernuous. *Bracts* deltate-attenuate to ovate-acuminate, scarious, brownish white, somewhat plicate-keeled, the smaller with a solitary prominent dark brown median nerve, the larger often with 1 or 2 additional less distinct shorter nerves on either side, 5—10 mm long, 3—5 mm wide, with minutely denticulate margins. *Pedicels* the colour of the perianth, sparingly minutely white flecked, the lowest up to

15 mm long. *Perianth* bright scarlet-red (RHS 39A) to orange scarlet, brownish orange inside the mouth, exceptionally thick and fleshy, with copious clear nectar, very shortly stipitate, articulated to the pedicel, averaging 35 mm long, 10—12 mm diam. at the rather truncate base, thence becoming markedly trigonous, gradually narrowing to 7—8 mm diam., slightly laterally compressed with the triangular opening at the mouth only 3—4 mm across; *outer segments* free ± 10 mm, with 3 somewhat obscure, darker coloured nerves becoming brownish at their confluent apex, with somewhat translucent paler margins, with the acute apices minutely denticulate, those of the lateral segments very slightly spreading then becoming sharply incurved and that of the lowest strongly recurved; *inner segments* themselves free but dorsally adnate to the outer, broader and somewhat less acute, pale yellowish with a raised reddish keel with 3 indistinct nerves confluent towards the minutely denticulate, orange-brown (orange-yellow inside), strongly spreading to recurved apex. *Filaments* filiform-flattened, lemon-yellow, the 3 inner narrower and lengthening before the 3 outer; *anthers* orange-brown, not or only slightly exserted. *Ovary* bright green, 6-grooved, narrowly ovoid-cylindric, 6·5 mm long, ± 3 mm diam. at the base, ± 2·5 mm diam. at the apex; *style* lemon-yellow, scarcely or up to 1 mm at length exserted; *stigma* white. *Seeds* dark to blackish brown, irregularly and variably triquetrous with thin wings, 5·5—7 mm long, ± 3 mm broad.

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SOUTH AFRICAN SPECIES OF CYNODON (GRAMINEAE)[1]

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Abstract

The genus *Cynodon* Rich. is represented in South Africa by *C. aethiopicus* Clayton et Harlan ($2n=18$), *C. dactylon* (L.) Pers. var. *dactylon* ($2n=36$), var. *aridus* Harlan et de Wet ($2=18$), var. *elegans* Rendle ($2n=36$) and var. *polevansii* (Stent) Harlan et de Wet ($2n=36$), *C. incompletus* Nees var. *incompletus* ($2n=18$) and var. *hirsutus* (Stent) de Wet et Harlan ($2n=18$), and *C. transvaalensis* Burtt-Davy ($2n=18$). Several sterile, triploid hybrids between *C. dactylon* var. *dactylon* and the diploid ($2n=18$) taxa were collected. One such hybrid is widely cultivated and known taxonomically as *C. magennisii* Hurcombe. The cultivated *C. bradleyi* Stent was shown to represent a hybrid between the two varieties of *C. incompletus*.

Uittreksel

SUID-AFRIKAANSE SOORTE VAN CYNODON (GRAMINEAE). Die geslag *Cynodon* Rich. word in Suid-Afrika verteenwoordig deur *C. aethiopicus* Clayton en Harlan ($2n=18$), *C. dactylon* (L.) Pers. var. *dactylon* ($2n=36$), var. *aridus* Harlan en de Wet ($2n=18$), var. *elegans* Rendle ($2n=36$) and var. *polevansii* (Stent) Harlan en de Wet ($2n=36$), *C. incompletus* Nees var. *incompletus* ($2n=18$) and var. *hirsutus* (Stent) de Wet en Harlan ($2n=18$) and *C. transvaalensis* Burtt-Davy ($2n=18$). Verskeie onvrugbare, triploiede kruisings tussen *C. dactylon* var. *dactylon* en die diploiede ($2n=18$) taksa was versamel. Een so 'n kruising word op groot skaal gekweek en is taksonomies as *C. magennisii* Hurcombe bekend. Die gekweekte *C. bradleyi* Stent word getoon 'n kruising tussen die twee varietete van *C. incompletus* te wees.

Introduction

The genus *Cynodon* Rich. is a small genus, confined primarily to the tropics and subtropics of the Old World, but with one species, the weedy *C. dactylon* (L.) Pers., extending almost continuously across all continents and islands between about 45° N and 45° S latitude. The genus is particularly variable in southern Africa where several taxa of uncertain taxonomic status were described (Stent, 1927). The relationships among these traditionally recognized species and varieties were studied.

Material and methods

Several hundred collections of *Cynodon* were studied in their natural habitats in southern Africa, and some 250 of these were grown from seeds or cuttings

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and transplanted to a uniform nursery at the Oklahoma Experiment Station, Stillwater. Herbarium specimens of these collections are filed with the Crop Evolution Laboratory, Department of Agronomy, University of Illinois. Hybrids were produced by W. L. Richardson using a modification of a technique described by Richardson (1958). Chromosome number and cytological behavior were determined from developing microspore mother cells stained with aceto-carmine. The morphological data were supplemented by studies of the *Cynodon* collections filed at Kew, England, and the Botanical Research Institute at Pretoria, South Africa.

Results

The South African respresentatives of *Cynodon* are usually subdivided among three non-rhizomatous taxa, *C. bradleyi* Stent, *C. hirsutus* Stent and *C. imcompletus* Nees, and four rhizomatous taxa, *C. dactylon*, *C. magennisii* Hurcombe, *C. plovansii* Stent and *C. transvaalensis* Burtt-Davy.

The non-rhizomatous taxa are closely allied to each other. *Cynodon bradleyi* is widely cultivated, and seem to have originated from a single population found growing wild in unbroken veld at Orange Grove, Johannesburg. Stent (1927) suggested that this species represents a hybrid between *C. hirsutus* and *C. dactylon*. Such an origin is unlikely, as the assumed parental species are diploid ($2n=18$) and tetraploid ($2n=36$) respectively, while *C. bradleyi* is a diploid. It resembles *C. hirsutus* in leaf pubescence and gross inflorescence structure, but the glumes are smaller. Typically, *C. hirsutus* has lower glumes that are about half as long as the spikelets, and upper glumes that are at least 3/4 the spikelet length, while the lower glume of *C. bradleyi* is about 1/3 and the upper glume about 1/2 as long as the spikelet. Stent (1927) described *C. hirsutus* var. *parviglumis* to include plants which have shorter glumes than the type. Several such populations were collected in the arid western Transvaal around Delareyville, and at Bloemfontein in the Orange Free State. Except that they are slightly less hairy, and have slightly longer leaves, these collections resemble *C. bradleyi* very closely. They also match in detail artificially produced hybrids between *C. hirsutus* and *C. incompletus*. These hybrids are fully fertile, and *C. bradleyi* crosses readily with *C. hirsutus* var. *parviglumis* to produce fertile hybrids.

Cynodon hirsutus and *C. incompletus* are closely allied morphologically, differing from each other primarily in degree of pubescence and glume size. Typical representatives of *C. incompletus* have leaves that are at most moderately pilose, lower glumes that are about 1/4 as long as the spikelet, and upper glumes that are slightly less than 1/2 the spikelet length. Hirsute leaves, and glumes that are 1/2 to 3/4 as long as the spikelet characterize *C. hirsutus*. These two taxa maintain their unity of type primarily because of ecological, and also to some

degree geographic isolation. *Cynodon incompletus* is widely distributed in the more arid regions across the Karroo, Orange Free State and West Transvaal, while *C. hursutus* is widely distributed in the Bushveld but also extends into the Highveld and the Karroo. Their distribution ranges overlap extensively in the western Transvaal, and natural hybrids are common where they grow together. Morphological and cytogenetical data indicate that the three non-rhizomatous South African taxa *C. bradleyi*, *C. hirsutus* and *C. incompletus* belong to a single species (Harlan et al., 1970).

The rhizomatous collections include both diploids and tetraploids. *Cynodon transvaalensis* is strictly diploid ($2n=18$). This species is widely cultivated as a lawn grass, with widely scattered, possibly natural populations in damp habitats across the southern and western Transvaal. These may represent relics of a once common wild species. It is very uniform morphologically. Leaves are narrowly linear and yellowish green, two characters that distinguish *C. transvaalensis* from all other *Cynodon* species. Inflorescences of *C. transvaalensis* are small, with rather loosely arranged spikelets, and somewhat resemble those of small, cultivated races of *C. dactylon*. Stent (1927) assumed that *C. transvaalensis* originated as a hybrid between *C. dactylon* and *C. hirsutus*. Attempts to cross *C. transvaalensis* with representatives of the non-rhizomatous complex failed, but it crossed readily with tetraploid and diploid *C. dactylon* to produce sterile hybrids. The cultivated triploid *C. magennisii* resembles some of the artificially produced hybrids in morphological detail, and probably originated from such a cross (Hurcombe, 1947).

Cynodon polevansii is narrowly endemic to arid habitats in the western Transvaal that are seasonally flooded. In its natural habitat *C. polevansii* is a compact plant with short, stiffly erect leaves, well developed rhizomes, and slender flowering culms bearing inflorescences of 2—4, often reflexed racemes. Because of its compact growth habit, and narrow leaves, Stent (1927) suggested close affinities with *C. transvaalensis*. When plants from the type locality were planted in our uniform nurseries, however, they resembled *C. dactylon* rather than *C. transvaalensis* more closely. From *C. dactylon* these plants differed primarily in having narrow, erect leaves, and from *C. transvaalensis* they differed very obviously in their more robust growth habit. All collections of *C. polevansii* are tetraploid, and this taxon crossed readily with collections of *C. dactylon* to produce fertile hybrids. Several obviously hybrid populations were collected from the type locality. For these reasons *C. polevansii* was transferred to *C. dactylon* as a variety by Harlan and de Wet (1969).

Cynodon dactylon is an extremely variable species, widely distributed across the world between about 45° N and 45° S latitude. The South African materials are of three very distinct morphological types. The widely cultivated lawn grass, which is also widely distributed as an urban and roadside weed, is a compact

plant with $2n=36$ chromosomes. Collections range in size from small races that are used as lawn grasses to robust weeds that produce flowering culms up to 20 cm tall. The common, native *C. dactylon* south of 12° S latitude, however, is a lax plant with slender rhizomes and inflorescence branches. These collections correspond exactly with the type of *C. dactylon* var. *elegans* Rendle, from Mossamedes in Angola (B). It is a tetraploid and extends from the coastal plains to the Highveld, across most of the veld types described by Acocks (1953). Diploids that resemble variety *elegans* in growth habit were collected at Middelburg in the Cape Province. Morphologically similar plants were also collected in Tanzania, Israel and India, and *C. dactylon* var. *aridus* was described by Harlan and de Wet (1969) to include these diploids.

Hybrids between *C. dactylon* var. *dactylon* and var. *elegans* are easy to produce and are fertile. Natural hybridization is not common, probably because these two varieties occupy different habitats, var. *dactylon* being a weed (Harlan and de Wet, 1965) while var. *elegans* forms part of the natural grass vegetation. The diploid, *C. dactylon* var. *aridus* crosses readily with the tetraploids to form sterile triploid hybrids. It was also crossed with *C. hirsutus*, *C. imcompletus* and *C. transvaalensis*. These hybrids are sterile with 0—6 univalents present during meiotic metaphase of microsporogenesis (Harlan et al., 1970).

Several collections from around Barberton and Tzaneen in the eastern Transvaal, resemble a robust *C. dactylon*, but are non-rhizomatous. These collections are diploid and belong with *C. aethiopicus* a species widely distributed along the rift valleys from South Africa to Ethiopia (Harlan, de Wet and Richardson, 1969; Clayton and Harlan, 1970). This species may be more common along the mountains in South Africa than would appear from the few specimens available in herbaria.

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BYDRAE TOT DIE MORFOLOGIE EN ANATOMIE VAN ROMULEA: III. DIE BLOEIWYSE EN BLOM

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Samevatting

Die romuleabloeiwyse bestaan uit een of meer monochasia met twee bloeistele in elke monochasium, en elke bloeisteel met 'n enkele blom, sittend gedra binne 'n twee-kleppige bloeiskede.

Verskeie anatomiese strukture van die blom word beskryf, bv. die septale nektarkliere, die stempels, blomdekepidermis en -mesofil, en die vaatstelsel. Die are van die styl en stempels toon dat die drie styltakke teenoor die meeldrade staan en nie met hulle alterneer nie soos Bentham en Hooker gemeen het. In elke dorsale naat van die vrugbeginsel is 'n gemeenskaplike aar vir die styl, meeldraad en die middel van die buite-blomdekblaar. Teenoor elke septum van die vrugbeginsel is 'n enkele aar wat die binne-blomdekblaar voorsien en ook die kantare vorm van die buite-blomdekblaar.

Meeste van die bg. kenmerke is konstant gevind by die ondersoekte species. Verskeie ander blom- en bloeisteelkenmerke kom voor wat sekere species of speciesgroepe onderskei, bv. lang silindriese blomdekbuise, 'n vergroeide helmdraadbuis, meer as ses stempels, of opgekrulde vrugstele. Daar word aan die hand gedoen dat die lg. te wyte is aan 'n verskil in die lignifikasie in die twee kante van die vrugsteel.

Abstract

CONTRIBUTION TO THE MORPHOLOGY AND ANATOMY OF ROMULEA: III. THE INFLORESCENCE AND FLOWER. The romulea inflorescence consists of one or more monochasia with two peduncles in each, and each peduncle bearing a single sessile flower within a two-valved spathe.

Several anatomical features of the flower are described, e.g. the septal nectaries, the stigmas, epidermis and mesophyll of the perianth, and the vascular system of the flower. The vascular bundles of the style and stigmas show that the three style branches are opposite the stamens and do not alternate with them as Bentham and Hooker supposed. In each dorsal suture of the ovary a single vascular strand is present which forms the bundles for the style, stamen and centre of the exterior perianth segment. Opposite each septum of the ovary another single strand occurs which supplies the interior perianth segment and forms the marginal veins of the exterior segment.

Most of the above-mentioned characters are constant in the species examined. Several other features of the flower and peduncle are of importance in distinguishing certain species or groups of species, e.g. long cylindrical perianth tubes, fused filaments, more than six stigmas, or coiled peduncles in the fruiting stage. It is suggested that the latter is caused by a difference in lignification along the two sides of the peduncle.

Inleiding

Gedurende 'n ondersoek vir die revisie van die Suid-Afrikaanse species van Romulea het sekere anatomiese aspekte en probleme i.v.m. die blom na vore gekom waaroor helderheid gesoek is.

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Daar is byvoorbeeld gesoek na die nektarkliere wat nie uitwendig in die blom sigbaar is nie. Ook is duidelikheid gesoek oor die aard van die vrugbeginselwand, deur die vaatbundelverloop na te gaan, en derdens, die verhouding tussen die styltakke en die meeldrade.

Die laasgenoemde is 'n belangrike probleem want Bentham en Hooker (1883) het dit beskou as een van die wesenlike kenmerke wat die tribus Moraeeae van die tribus Sisyrinchieae onderskei: by die eersgenoemde is die drie styltakke teenoor die meeldrade en by die Sisyrinchieae alternerend daarmee (d.i. bokant die septa van die vrugbeginsel). Pax (1888) en Diels (1930) was twyfelagtig of die styltakke by „al die ander" met die meeldrade alterneer. Lewis (1954) p. 105 het aan die hand gegee dat Pax se idee dat die styltakke by die Sisyrinchieae 'n torsie ondergaan, verdere ondersoek regverdig. Aangesien so 'n ondersoek, sover vasgestel kon word, nog nie gedoen is nie, is die toestand by Romulea, een van die Sisyrinchieae, nagegaan.

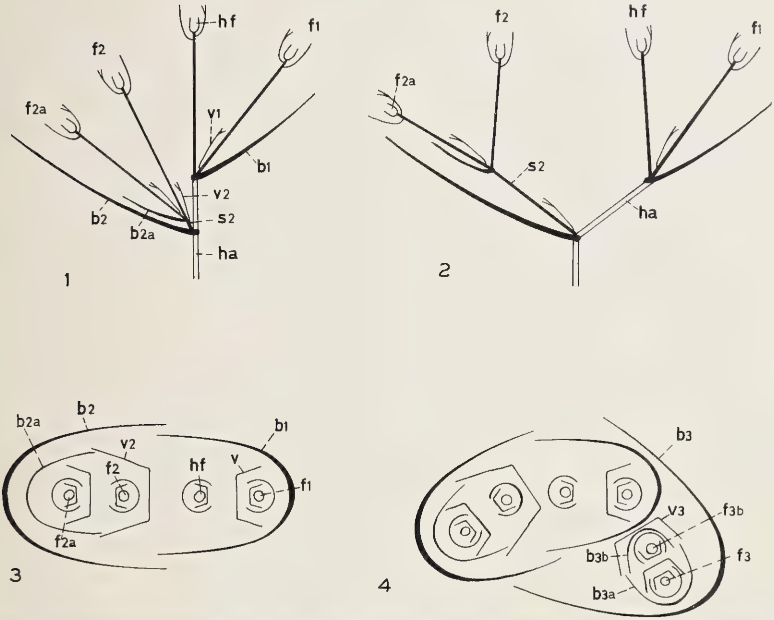
Materiaal en Metodes

Om 'n goeie oorsig oor die bloeiwyse en blombou van Romulea te verkry, is blomme van onder andere die volgende species, verteenwoordigend van agt seksies van die genus, ondersoek: *R. atrandra* Lewis, *R. dichtoma* Bak., *R. hirsuta* Bak., *R. minutiflora* Klatt, *R. monadelpha* Bak., *R. pratensis* n. sp. ms. nom., *R. rosea* Eckl. en *R. tabularis* Beg.

Gedissekteerde bloeiwyses is met 'n stereo-ontleedmikroskoop ondersoek. Vir die vaatskelet van die blom en die nektarkliere is mikrotoomsneë 15 μ dik gesny, gekleur met safranien en vaste groen of Delafield se hematoksilien, en permanent gemaak. Hele blomdekke is gefikseer en met chloraalhidraat deurskynend gemaak om hul vaatskelet na te gaan. Vir style is dieselfde metode gebruik. Vrugstele is in die lengte gesplits en die helftes apart gemasereer om die veselkrimping in die twee kante te ondersoek.

Ondersoek

Die Bloeiwyse. Die blomme, elk enkelstandig aan die top van 'n bloeisteel, word sittend of byna sittend gedra binne 'n twee-kleppige bloeiskede. Die bloeistele sluit die hoofas en sytakke af en kom in pare voor, elke paar in 'n monochasiale rangskikking. Die bloeivolgorde is basipetaal: die eerste blom om te ontwikkel (hf in fig. 1—3) is geleë aan die top van die hoofas (ha) en die tweede van die paar (f1) aan die einde van die boonste sytak. 'n Tweede paar bloeistele sluit die tweede hoogste sytak (f2) en dié se sytak van die tweede orde (f2a) af. Hierdie sytak herhaal dus die verhouding in die hoofas en die boonste sytak (fig. 1–3). Soms word die tweede bloeisteel van 'n paar in die oksel van die derde blaar van 'n sytak gedra (f3b in oksel van b3b, fig. 4).



Die Romulea-bloeiwyse. Fig. 1, algemene skema, diagrammaties, met twee pare blomme; die internodia tussen die blom, steelblaar en skutblaar is effens verleng; blom f (2) is op die tweede syas van bo, en f (2a) op 'n syas van die tweede orde. Fig. 2, van *R. dichotoma*, met die hoofas, ha, na die kant gestoot en die syas S (2) verleng. Fig. 3, grondplan van fig. 1, in distigiese rangskikking. Fig. 4, by *R. gigantea*, met drie pare blomme, spirodistigies; blom f (3b) is in die oksel van die derde blaar van die derde syas: b1, b2, b3, blare op hoofas; b 2a, b 3a, tweede blare (meestal vliesig) van syasse; b 3b, derde blaar van derde syas; f1, f2, f3, blomme op syasse van die eerste orde. f 2a, f 3b, blomme op syasse van die tweede orde; ha, hoofas; hf, blom op hoofas; S2, tweede hoogste syas; v1, v2, v3, profille van syasse.

By sommige species word 'n derde en selfs 'n vierde paar bloeistele gevorm in die oksels van die nog laer stingelblare (fig. 4). Soms is daar, bv. by *R. minutiflora*, 'n derde blomknop op 'n sytak van die derde orde aanwesig, wat egter nie tot bloei ontwikkel nie.

Hierdie blomrangskikking is konstant by die Suid-Afrikaanse Romulea-species en moontlik dwarsdeur die genus—vergelyk Haeckel (1931 p. 18–19) wat dieselfde tipe bloeiwyse aangee vir *R. bulbocodium* Seb. et Maur., waar egter slegs die boonste paar blomknoppe tot blomme ontwikkel. (Sy het ongelukkig in haar fig. 12 die blomme van sytak II verkeerdom geannoteer: haar blom IIa stel die eerste blom en II die tweede blom van die blompaar voor.

Ook is annotasies IIIa en IIIb omgeruil.) Sy toon verder dat die Romulea-bloeiwyse verwant is aan die van Crocus, waar dit egter nog meer gereduseer is.

Die Romulea-bloeiwyse verteenwoordig 'n erg gereduseerde vorm van 'n Iridaceae-bloeiwyse. Volgens Lewis (1954 p. 105) kom by een of twee species van Hesperantha en Geissorhiza gereduseerde bloeiwyses voor wat baie soos dié van Romulea is, met die hoofas en sytakke almal afgesluit met 'n enkele blom. Of hieruit afgelei mag word dat Lewis gemeen het dat die Romulea-bloeiwyse terug te lei is na die aar van die Ixieae (waaronder sy Romulea en Syringodea wou plaas) is nie duidelik nie. Die eindstandige blom van Romulea is waarskynlik slegs skynbaar terminaal, iets wat reeds deur Haeckel (1931) vir die Iridoideae en Crocoideae en deur Weimarck (1939) vir *Aristea singularis* gepostuleer is. Geen spore van 'n gereduseerde stingeltop kon egter by enige van die Romulea-species gevind word nie.

Die enigste variasies wat by die Romulea-bloeiwyses voorkom, is in die aantal bloeistele, en dus blomme wat ontwikkel, die lengte van die sytakke, in die torsie van die spruit by die hoërstaande species (spirodistigies teenoor distigies (fig. 3, 4), en die aard van die skutblaar en steelblaar onder die blom. Die aantal blomme is taamlik konstant by sommige species maar by ander word dit grootliks bepaal deur omgewingsfaktore en ook die ouderdom van die plant, daar jonger plante baiemaal minder blomme vorm. Dikwels ontwikkel die tweede blom van 'n laer paar bloeistele nie. By hoogstaande species met kort stingels, van bv. die seksies Roseae, Atrandrae en Bicarinatae, is die sytakke wat die bloeistele dra, baie kort en verberg. By seksies waar verlengde stingels voorkom, bv. die Hirsutae, Ciliatae, en Aggregatae, is die sytakke meestal 10—40 mm lank. By *R. dichotoma* is die sytakke net so sterk ontwikkel as die hoofas en stoot hulle die laasgenoemde effens na die een kant, sodat die vertakking digotoom voorkom (fig. 2).

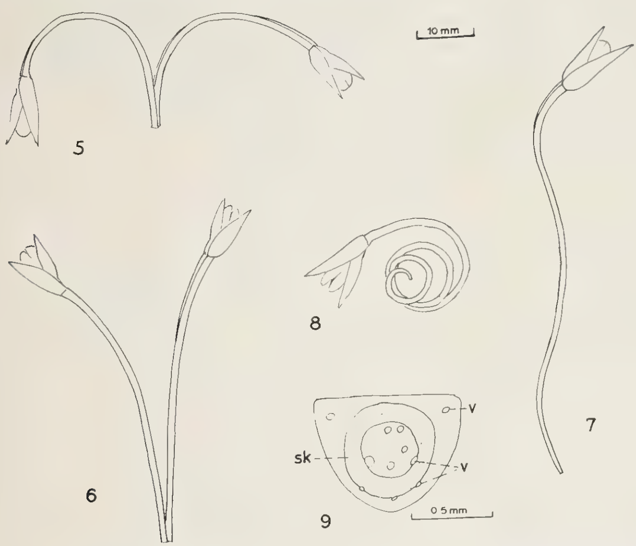
Die bloeiskede. Die skutblaar en steelblaar (profil, skutblaartjie of bracteola) vorm saam die tweekleppige bloeiskede direk onder die blom. Die internodia tussen hulle en die blom is gereduseer. Die steelblaar is dikwels swak twee-kielig en effens uitgerand, wat volgens sommige sy dubbele aard aantoon en volgens ander veroorsaak is deur drukking in die knop.

Die skutblaar en steelblaar lewer kenmerke wat bruikbaar is vir die uitkenning van soorte. Kenmerkend van die steelblare van 'n aantal species en van die skutblare van sommige, is hul vliesige rande wat uit 'n paar kleurlose sellae bestaan, met hier en daar 'n groepie grootsellige dikwandige sklereïede met 'n bruin selinhoud, wat aan die vliesige blaarrand 'n fyn-gestreepte of gespikkelde voorkoms gee. By 'n aantal species kom vliesige rande sonder spikkels of strepies voor. By die seksies Tortuosae en Macowania is beide blare grotendeels vliesig. By die Bicarinatae het die skutblaar 'n sterk middelaar en 'n kiel, en is die steelblaar twee-kielig met 'n sterk aar in elke kiel.

Die bloeisteel. Behalwe vir die skutblaar en die steelblaar onder die blom en 'n klein profil aan die basis van die tweede bloeisteel, is die bloeisteel kaal. By sommige species is die bloeisteel byna tereet en by ander semitereet (fig. 9), met die twee plat kante (adaksiale kante) van 'n paar bloeistele na mekaar gekeer. Die twee steelblare van 'n paar bloeistele staan rug teen rug (fig. 1—4).

Die vrugsteel. Die gedrag van die bloeistele na antese verskil by die seksies. By die meeste raak die bloeistele teruggebuig kort na antese, met die plat kant van die semiterete bloeisteel aan die buitekant van die boog. Hierdeur word die ontwikkelende vrug nader na die grond gebring of selfs in die grond gedruk. Wanneer die bloeisteel met die ryp vrug uitdroog, buig dit weer orent en reguit (fig. 5, 6), behalwe vir die species van die seksies Tortuosae en Atrandrae.

Marloth (1915 p. 147) het reeds die reguitwording van die vrugsteel van *R. rosea* beskryf, maar Stopp (1958) was onder indruk dat die vrugte basikarp bly, ook wanneer die vrugte ryp is en oopsplits. Wat werklik gebeur is dat die ryp vrugstele van baie species herhaaldelike higroskopiese bewegings uitvoer: wanneer hulle uitdroog word hulle reguit, en ná benatting buig hulle weer af. Moontlik het Stopp slegs klam bloeistele gesien.



Vrugstele van Romulea. Fig. 5, 6, van *R. citrina*, klam en droog onderskeidelik. Fig. 7, 8 van *R. atrandra*, klam en droog onderskeidelik. Fig. 9, dwarssnee deur vrugsteel van *R. atrandra:* sk, sklerenchiem met minder lignifikasie aan die plat kant; v, vaatbundels.

By die reeds genoemde Tortuosae en Atrandrae toon die droë vrugstele besonder sterk higroskopiese bewegings. Tydens die uitdroging buig hulle van 'n halfregop of effens gebuigde posisie met die plat kant aan die buitekant van die boog, regoor na die teenoorgestelde kant en word hulle soos 'n horlosieveer opgekrul met die plat kant aan die binnekant van die spiraal (fig. 7, 8). In nat weer buig hulle weer terug. Hierdie heen en weer bewegings vind ook herhaaldelik plaas.

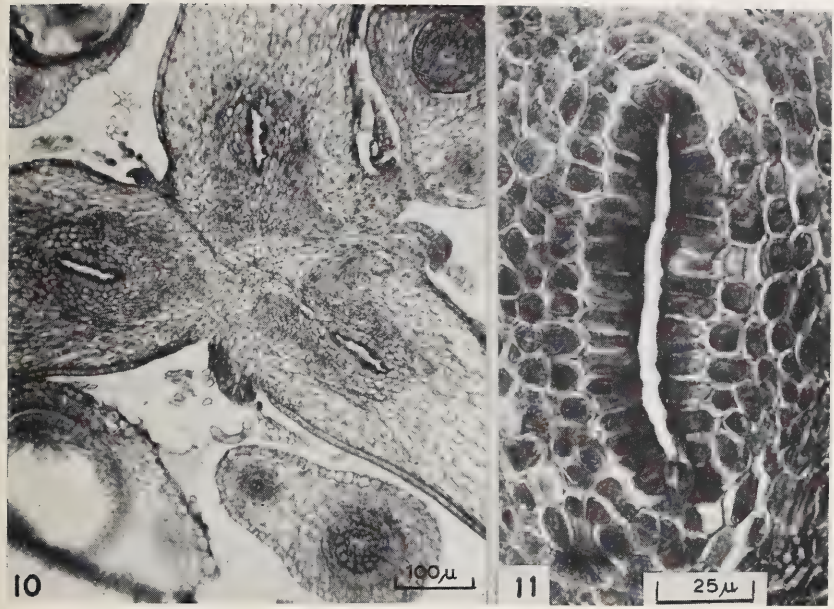
Die higroskopiese bewegings word veroorsaak deur 'n ongelyke verkorting en verlenging langs die plat en afgeronde sye van die vrugsteel, in 'n silinder van sklerenchiemvesels wat 'n endjie onder die epidermis geleë is. In die plat kant krimp en rek die vesels meer in die lengte tydens veranderings van hul waterinhoud as aan die teenoorgestelde kant. Sien tabel 1, waar die eersgenoemde twee species in die tabel, behorende tot die Atrandrae, vergelyk word met *R. minutiflora*, wat bewegings slegs van krom na reguit en terug uitvoer.

TABEL 1.
Lengtes van stukkies bloeistele, in die lengte gesplits en nat en droog gemeet in millimeters.

	Plat kant		Afgeronde kant	
	Nat	Droog	Nat	Droog
R. atrandra	10·0	8·5	10·0	10·2
R. komsbergensis	10·0	8·0	10·0	9·5
R. minutiflora	10·0	9·3	10·0	9·6

Wanneer die plat en afgeronde kante apart gemasereer is, kan die verkorting en uitrekking van individuele vesels mikroskopies besigtig word: vesels van *R. atrandra* uit die plat kant verkort met 10—25% wanneer die water waarin hulle gemonteer is, vervang word met 100% alkohol—terwyl dié aan die afgeronde kant feitlik nie krimp nie.

Dwarssneë van die bloeistele in floroglusien gekleur, toon die moontlike rede vir die verskil in verkorting: die vesels aan die afgeronde kant is baie meer verhout as aan die plat kant (fig. 9). Dit beteken dat die vesels aan die plat kant meer water in die matriks van die selwande besit, wat in die vesels van die afgeronde kant tot groter mate verplaas is met lignien. Wanneer die water deur die alkohol verwyder word, krimp die vesels aan die plat kant. Verder is die waarskynlikheid nie uitgesluit nie dat die verskille in krimping ook deels veroorsaak word deur bepaalde oriëntasies van die sellulosefibrille in die veselwande.



Septale nektarieë van Romulea. Fig. 10, dwarssnee deur die sentrale deel van die vrugbeginseltop by *R. atrandra*. Fig. 11, een nektarie in dwarssnee by *R. pratensis*.

Sekere species toon geen higroskopiese beweging nie. By bv. *R. cruciata*, *R. setifolia*, en *R. aquatica* bly die bloeistele min of meer reguit en regop na die antese. By *R. sladenii*, *R. dichotoma* en nog 'n paar word die bloeistele na antese wyduitspreidend vanaf hul basisse en bly so, of hulle nat of droog is.
Die septale nektarkliere. Volgens Elliot (1891) word die nektar by Romulea deur die basisse van die helmdrade gesekreteer. Daar hierdie verklaring, sover vasgestel kon word, nooit weerspreek is nie, word hieroor gerapporteer.

Naby die top van die vrugbeginsel is die versmelting van die vrugblare onvolledig en kom in elk van die drie tussenskotte 'n smal vertikale spleet voor, omring deur 'n epidermis en verskeie lae klein plasmaryke selle (fig. 10, 11). Hierdie is die septale nektarkliere wat ooreenstem met dié van Crocus (Böhmker 1917). Aan die kant na die sentrale as gekeer is elke nektarie omring deur 'n aantal klein aartjies wat die uiteindelike takke is van die ventrale vrugblaarare.

Effens hoër dwarssneë (fig. 13iii) toon dat elke nektarie deur 'n smal spleetjie uitmond in die bodem van die blomdek aan die basis van die styl, waar die

nektar opgegaar word. Dáár word die nektar beskerm deur eensellige epidermale hare wat van die basis van die helmdrade en dikwels ook van die binne-epidermis van die blomdekbuis uitgroei. Slegs by *R. monadelpha* met vergroeide helmdrade is hare heeltemal afwesig, en word die nektar deur die helmdraadbuis beskerm.

Die vaatskelet van die blom. Die vaatskelet van die bloeisteel (fig. 9) bestaan uit 'n aantal verspreide vaatbundels binnekant 'n silinder prosenchimatiese parenchiemweefsel wat later verhout, en 'n aantal perifere vaatbundels buitekant hierdie silinder.

Naby die top van die bloeisteel vertak die perifere bundels en verdeel hulle om twee kringe bundels te vorm: die buitenstes word die spore van die skutblaar onder die blom, en die binneste kring dié van die steelblaar.

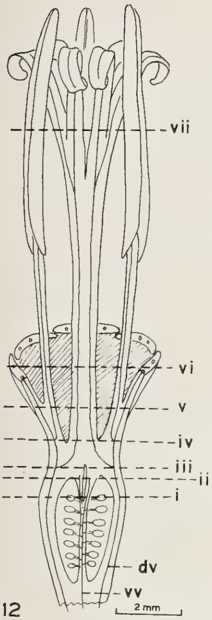
Drie van die sentrale bundels loop effens na buite en dan op in die drie dorsale nate van die vrugbeginsel. Daarna loop nog drie sentrale bundels, alternerend met die eerste drie, na buite, en word die laterale vrugblaarbundels.

Die origе sentrale bundels loop na die senter van die bloeisteeltop en vorm daar 'n groot komplekse bundelgroep wat uit verskeie xileem- en floëemgroepe bestaan. Dit loop regop in die sentrale as van die vrugbeginsel in en deel in drie dele om drie ventrale vrugblaarbundels te vorm. In hul opwaartse loop vertak hulle herhaaldelik om 'n aartjie vir elke saadknop te verskaf, en naby die top van die vrugbeginsel voorsien die oorblywende takkies die septale nektarkliere (fig. 13i). Hulle eindig meestal net bo die nektarklierweefsel. By *R. monadelpha* egter en miskien ook by ander grootblom-soorte loop 'n paar van hulle tot in die basis van die styl waar hulle dan verdwyn.

Die vrugbeginselwand het die ses reeds genoemde are: een in die dorsale naat van elke vrugblaar (dv in fig. 13i) en een teenoor elke tussenskot (lv in 13i). Hierdie bearing stem ooreen met dié van Iris (Eames en MacDaniels 1947).

Die aar (dv) in elke dorsale vrugblaarnaat, hier genoem 'n dorsale vrugblaarbundel, is in werklikheid 'n gesamentlike bundel vir die vrugblaar, meeldraad, en middel van die buite-blomdekblaar. Aan die top van die vrugbeginsel vertak 'n stylbundel hieruit na binne en loop op in die styl (s in fig. 13iii, iv).

Vaatskelet van die Romulea-blom. Fig. 12, 'n nie-mediane lengtesnee deur 'n blom, diagrammaties, om die mediane aar van die buitenste blomdekblaar en die meeldraad- en stylare te toon. Fig. 13, 1-vii, diagrammatiese dwarssneë deur blom op hoogtes aangetoon in fig. 12. Fig. 14, halwe blomdek, om die hoofblomdekare te toon. Fig. 15, stempels en top van styl van *R. atrandra*, oopgesplits, met helmknopposisies aangetoon. Fig. 16, stempels en styltop van *R. komsbergensis*, oopgesplits: dv, dorsale vrugblaarbundel; e, buite-blomdekblaar; el, sytak wat verdwyn, van buite-blomdekblaar; ep, mediane bundel van buite-blomdekblaar; h, helmknop; in, binneste blomdekblaar; il, sytak van laterale vrugblaarbundel; ip, mediane bundel van binne-blomdekblaar; lv, laterale vrugblaarbundel; m, meeldraadbundel; n, septale nektarie; on, opening van nektarie; s, stylbundel; st, stempelbundel; til, takke van il wat na buite- en binne-blomdekblare loop; vv, takke van ventrale vrugblaarbundels.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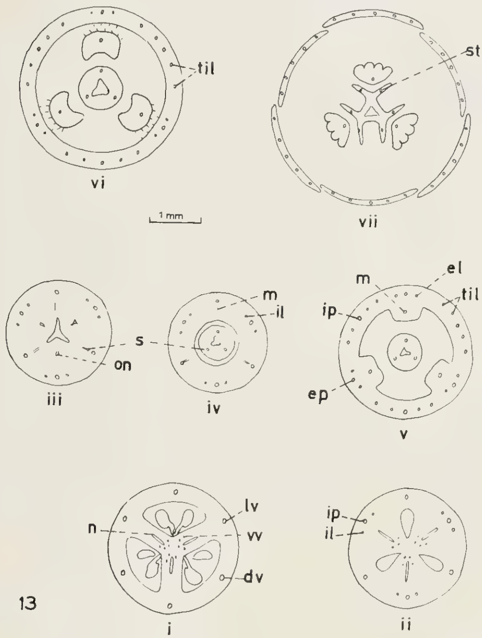
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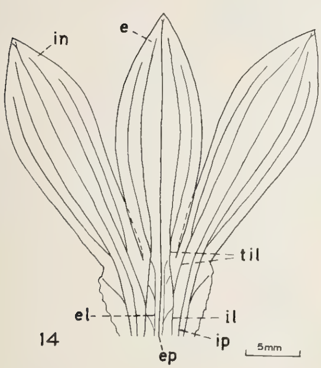
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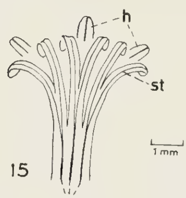
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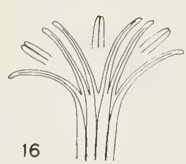


16

By die meeste species ontvang die styl slegs die drie are, behalwe by die reeds genoemde *R. monadelpha*.

Die oorblywende gesamentlike meeldraad- en blomdekbundel vertak weer en vorm, op één radius, 'n meeldraadbundel na binne en 'n buite-blomdekbundel (fig. 13iv). By die vergroeide helmdrade van *R. monadelpha* egter, ontvang die helmdraadbuis die drie meeldraadbundels asook verskeie kleiner bundels (de Vos 1970 fig. 4), wat takke is van die are van die binne-blomdekblare. Hoog in die helmdraadbuis eindig die klein bundels blind, terwyl die drie egte meeldraadbundels in die helmbindsel opstrek. Of hieruit afgelei mag word dat die helmdraadbuis 'n blomdekuitgroeisel is, is onseker—miskien sal ontogenetiese studies uitsluitsel gee.

Die oorblywende buite-blomdekbundel vertak tangensiaal in drie langsmekaarliggende takke (fig. 13v). Die middelste (ep in fig. 14) word die mediane aar van die buite-blomdekblaar, maar die are (el) weerskante loop gou dood deur met die are gemerk til in fig. 14 te verenig.

Die bundel in die vrugbeginselwand teenoor elke septum, hier genoem die laterale vrugblaarbundel (lv in fig. 13i) is in werklikheid 'n gesamentlike laterale vrugblaar- en blomdekbundel. Op die hoogte van die vrughoktoppe vertak dit tangensiaal in drie langsmekaarliggende takke (fig. 13iii), en loop so die blomdekbuis in. Die middelste word die mediane aar van die binne-blomdekblaar, en die twee weerskante (il) vurk en verskaf 'n bundel vir die buite- en die binne-blomdekblaar (til in fig. 13vi en 14). Die laterale vrugblaarbundel behoort dus nie net aan twee vrugblare nie, maar ook aan twee blomdekblare.

Die aarvoorsiening vir die twee blomdekkranse is dus verskillend: al die are van die binne-blomdekblaar is afkomstig van die laterale vrugblaarbundel, maar slegs die mediane aar van die buite-blomdekblaar en sy takke kom van die dorsale bundel, terwyl die groot are weerskante deur die laterale vrugblaarbundel voorsien word. D.w.s. elke binne-blomdekblaar word deur één spoor voorsien, maar elke buite-blomdekblaar deur drie spore. Hierdie is vergelykbaar met die toestand by die kroon- en kelkblare van baie dikotiele.

By species met medium en groot blomme wat vyf of soms sewe hoofare per blomdekblaar het, vurk die kantare (til) weer (fig. 14) om die twee of drie groot kantare te verskaf. Uit al die groot are vertak klein are wat veervormig na die rande van die blomdekblaar loop en blind eindig as enkelryige spiraaltracheïede. Die mediane aar vurk egter digotoom aan die top net voor dit eindig (fig. 14). Skuins anastomoses tussen die are kom voor.

Die verhouding tussen die stylvlakke en die meeldrade

Behalwe vir *R. multifida* De Vos en 'n variëteit van *R. tortilis* Bak. wat veelvertakte style en meer as ses stempels het, is die styl naby die top in drie twee-spletige takke verdeel en is daar ses stempels. Die stempels, wat effens

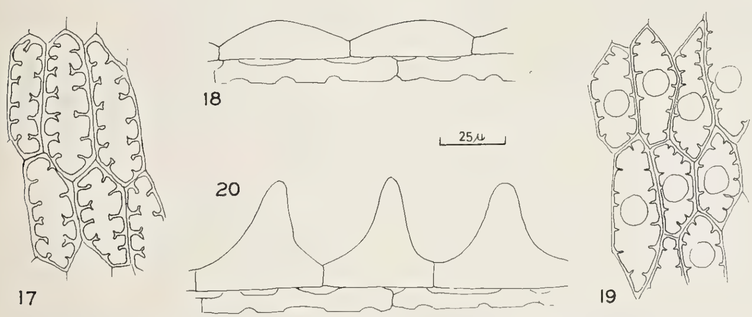
later as die meeldrade ryp word, beslaan die hele lengte van die styltakke. In die jong toestand is hulle konduplikaat, maar later vou hulle meestal tot 'n mindere of meerdere mate oop en is dan tongvormig en bo gegroef, met 'n digte ry marginale eensellige papillae.

By die meeste romuleas kom die eerste vertakking van die styl laer af voor as die verdere splitsing van elk van die drie takke (fig. 15). Die primêre asse kan dus uitwendig onderskei word. By *R. komsbergensis* De Vos egter is die ses takke ewe lank, sodat uitwendig nie gesien kan word watter paar stempels aan dieselfde primêre styltak behoort nie (fig. 16).

Na behandeling van die style met chloraalhidraat is die vertakkings van die drie stylare duidelik waarneembaar. Elkeen van die drie stylare vertak in twee om die ses stempels te voorsien en dit is duidelik watter paar stempels aan dieselfde primêre styltak behoort, selfs by dié species met ewelang styltakke (fig. 15, 16).

By species met kort style en stempels laer as die helmknoppe geleë, is elke primêre styltak se twee stempels wyduitspreidend en steek hulle weerskante verby die meeldraad wat teenoor die styltak staan (fig. 15, 16). Dit beteken dat die twee stempels wat styf teen mekaar tussen die helmknoppe uitsteek, aan twee aangrensende styltakke (en dus aan twee vrugblare) behoort en dat elke primêre styltak teenoor die meeldraad en ook bokant die vrugbeginselhok (d.w.s. die dorsale naat van die vrugblaar) staan. Dit stem ooreen met die toestand by Iris en die ander Moraeeae.

By die romuleas met styltakke wat bo die helmknoppe uitsteek, word die twee stempels van een styltak nie weg van mekaar gedruk nie, en staan die pare stempels naby mekaar. Die drie primêre styltakke staan dan soms bokant die



Blomdekepidermis van Romulea. Fig. 17, 18, van *R. dichotoma*, oppervlakkig en in lengtesnee onderskeidelik. Fig. 19, 20, van *R. tabularis*, oppervlakkig en in lengtesnee onderskeidelik.

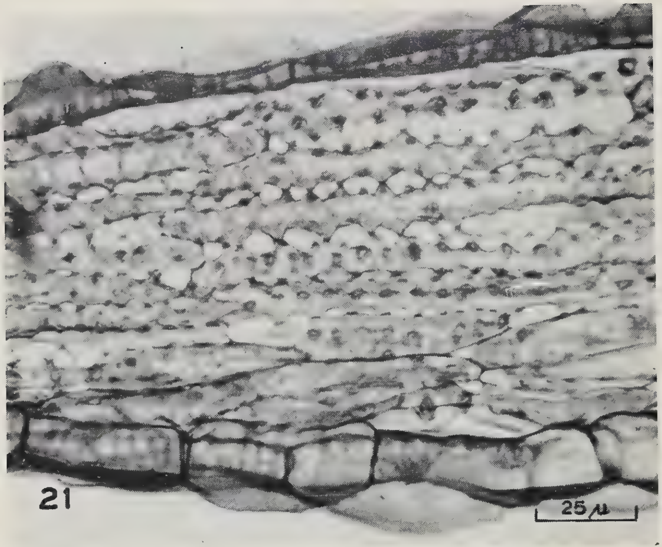


Fig. 21. Lengtesnee deur blomdek van *R. minutiflora.*

meeldrade of alterneer soms met hulle, deur 'n effense draaiing van die styl. *Die blomdekepidermis en -mesofil.* Die blomkleure van die romuleas word veroorsaak deur rooi, pienk, pers of geel gekleurde selsap in die epidermisselle van die blomdekblare. 'n Groen kleur aan die buitekant is te wyte aan chloroplaste in die abaksiale subepidermale mesofil.

Nader aan die basis van die blomdekblare kom verlengde epidermisselle voor met gladde wande. Hoër op word die selle geleidelik korter en by die meeste species toon die antiklinale epidermisselwande kort ingroeisels na binne in die vorm van lyste (fig. 17, 19). By *dichotoma* het die lyste 'n breër vry randjie wat soms gesplete is (fig. 17). By sommige species ontbreek sulke ingroeisels of is hulle slegs in die adaksiale epidermis aanwesig.

Die adaksiale epidermisselle, en soms ook die abaksiale, is konveks na buite opgeswel, bv. *R. dichotoma* (fig. 18), of elke sel besit 'n sentrale papilla, bv. *R. tabularis* (fig. 19, 20). Die konvekse rondings veroorsaak blink blomdekblare, terwyl die aanwesigheid van papillae 'n dowwe voorkoms gee.

Die mesofil van die blomdekblare bestaan uit verlengde parenchiemselle wat op vele plekke langs hul lengtewande van mekaar getrek is om lang rye intersellulêre ruimtes te vorm (fig. 21). Die ruimtes vergroot waarskynlik gedurende die daaglikse oop- en toegaan van die blom.

Die daaglikse blomdekbewegings is termonasties en vind plaas oor die hele blomdekblaar, van 'n toe-blom-stadium tot 'n toestand waarin die blomdekblare meestal teruggebuig is. Die bewegings is te wyte aan lengtestrekkings van die selle in die ad- en abaksiale kante van die blomdek om die beurt, en veroorsaak 'n blomvergroting van tot 5 mm by groot blomme, oor die ongeveer vier dae van die oop- en toegaan.

Bespreking

Heelparty van die kenmerke wat hier beskryf is, soos die bloeiwyse, die nektarkliere en die vaatskelet van die blom, is konstant by die Suid-Afrikaanse romuleas en moontlik ook dwarsdeur die genus. Hoewel hulle dus nie bruikbaar is vir die indeling van die species nie, is die kenmerke nogtans van algemene belang vir die genus. Byvoorbeeld, die enkele gemeenskaplike are in die dorsale nate en teenoor die septa van die vrugbeginsel, sou aantoon, volgens die sienswyse van verskeie navorsers waaronder Douglas (1944), dat die vrugbeginselwand uit die vergroeide basisse van die blomkranse bestaan.

Die vaatskelet van die styl en stempels toon dat die drie styltakke met hul stempelpare teenoor die meeldrade staan, net soos by die Moraeeae. Bentham en Hooker (1883) se sienswyse dat by die tribus Sisyrinchieae (waaronder hulle Romulea geplaas het) die styltakke met die meeldrade alterneer en bokant die septa van die vrugbeginsel staan, kan dus nie as altyd geldend aanvaar word nie. Pax (1888) en Diels (1930) was reg in hul vermoede dat die styltakke nie by alle Sisyrinchieae met die meeldrade alterneer nie. Slegs by 'n paar van daardie Romulea-species waar die stempels bokant die meeldrade verhef is, is die styltakke alternerend met die meeldrade, deur 'n effense torsie van die styl.

Alhoewel die blomkenmerke by Romulea oor die algemeen meer konstant is as die vegetatiewe kenmerke, is daar tog verskeie afwykende blomkenmerke wat sekere species of speciesgroepe van die ander onderskei. Byvoorbeeld, die lang silindriese blomdekbuise onderskei die seksies Macowania en Lomurea van die ander; *R. monadelpha* word deur sy vergroeide helmdrade onderskei (de Vos 1970); *R. multifida* word gekenmerk deur meer as ses stempels; by *R. aquatica* Lewis en *R. diversiformis* De Vos verskil die twee blomdekkranse heelwat in vorm en grootte; *R. flexuosa* Klatt het verlengde helmbindsels wat bo die stuifmeelsakkies uitsteek.

Die blomgrootte varieer tussen sekere perke vir elke species: sommige, bv. *R. minutiflora* en *R. monadelpha* het 'n klein variasieruimte, terwyl dié van ander, bv. *R. flava*, so groot is dat twee variëteite daarvoor beskryf is.

Die blomkleur en die merke in die keel van die blomdek, asook die merke en kleur aan die buitekant van die buite-blomdekblare is konstant by sommige

species en varieer by ander. Weens die variasie kan die blomkleur nie gebruik word om die genus in seksies in te deel nie, soos Baker (1896) gedoen het.

Klatt (1865–66) het die genus Trichonema, die destydse naam vir Romulea, in twee groepe ingedeel: (1) species met die meeldrade gelyk met die stempels of laer, en (2) species met stempels wat bo die meeldrade uitsteek. Hierdie kenmerk varieer in verskeie Kaapse species, en kan dus ook nie gebruik word om die genus in seksies in te deel nie.

Die skutblaar en steelblaar onder die blom lewer heelwat diagnostiese kenmerke, na gelang van die groenheid daarvan, die membraneuse rande en die breër are wat by sommige aanwesig is. Ook is die gedrag van die bloeisteel ná antese (of dit reguit bly, of eers afbuig en later by uitdroging reguit word of opkrul) kenmerke wat bepaalde seksies onderskei.

Dankbetuiging

My hartlike dank gaan aan die W.N.N.R. en die Universiteit van Stellenbosch vir toelaes om die materiaal te versamel, die direkteure van vele herbaria in die Republiek en in die buiteland, vir toestemming om hul materiaal te ondersoek, aan die kurator van die Universiteit van Stellenbosch se botaniese tuin vir die versorging van die plante, aan mnr. G. C. Crafford vir die neem van die foto's, en aan prof. P. G. Jordaan en mnr. J. A. van der Walt vir die oorlees van dele van die manuskripte.

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Useful Plants

In the botanical fraternity, among the teachers, and even more noticeably among the taught, there exists a strange morality whereby members of the plant kingdom, once having been touched by commerce or comestibility, are no longer considered fit for serious study or discussion. This is not to suggest that there is a need to initiate options in "Economic Botany", which develop, apparently inevitably, their own special mystique, a kind of *materia medica*. Rather one might advocate just a little more tolerance, a little more awareness of professing botanists, of those plants which have an undoubted impact on man's affairs. The books reviewed below deal with completely different aspects of domestic plants, but each is worthy of a place on the botanists' bookshelf.

The Domestication and Exploitation of Plants and Animals ed. by Peter T. Ucko and G. W. Dimbleby, with pp. xxvi + 581, 8 plates + 72 line figures and maps. London: Gerald Duckworth & Co., 1969. Price £37.35.

In May 1968 the Research Seminar in Archaeology and Related Subjects met a London University to discuss the history of domesticated plants and animals. The proceedings of this meeting have been considerably expanded and, unlike many published symposia, rendered into a most successful and integrated book. This is undoubtedly a work of major significance and forms a worthy successor to those of de Candolle, Vavilov and Hutchinson.

The papers are divided about equally between plants, animals and general topics. Of particular interest to botanists are "The Geological Background of Plant Domestication" by T. G. Hawkes, "The Progenitors of Wheat and Barley . . ." by Daniel Zohary, "History and Ethnography of some West Indian Starches" by W. C. Sturtevant, "The Archaeological Evidence for the Domestication of Plants: Methods and Problems" by J. M. Renfrew. "The Origins of Yam Cultivation" by T. Alexander & D. E. Coursey, and "The Origin, Variability and Spread of the Groundnut" by A. Krapovickas.

However, this book should also be considered from the wider standpoint of the insight it gives into the utilisation of biological resources. It gives a very clear picture of the width and precision of modern archaeological investigations and demonstrates the overwhelming effect of environment upon the growth of civilisations.

The book is exceptionally well printed and provided with extensive bibliographies and an adequate general index.

Tropical Crops: Dicotyledons by J. W. Purseglove, with pp. xxi + 719, 102 full page line illustrations, 2 vols. London & Harlow: Longmans, Green & Co., 1968. R5.5.

These two volumes contain a concise and systematic account of the botany and agronomy of the major crop plants grown on a field scale in tropical to warm temperate climates (not, as stated on the dust jacket, between the tropics of Cancer and Capricorn). The arrangement is alphabetical by families and genera, which, together with an appendix of synonyms and a comprehensive index, makes for ease of reference. Where appropriate, keys are given to species. The space devoted to each plant is related to its importance as a world crop.

The origin, ecology and distribution of each crop is well described, including a discussion of the relation of cultivars to the species and lines of improvement. The chromosome number is recorded as well as a short account of such features as the general morphology, pollination and germination. There is also a synopsis of the uses, husbandry, propagation and major diseases.

Longmans have maintained their customary very high standard of a clear and attractive format and substantial binding. The full page illustrations are also of a high quality. Altogether this is a most useful reference work which should find a place in every library and herbarium.

THE OXFORD BOOK OF FOOD PLANTS. Text by S. G. Harrison, G. B. Masefield and M. Wallis, illustrations by B. E. Nicholson, with pp. viii + 206 (including 95 pages in colour). Oxford: Oxford University Press, 1969. £2.75.

"From these pages, the townsman can learn what kinds of plants provide the foods which appear in his local shops; the inhabitant of any country can discover the origin of those food plants which are imported into it; and everyone can learn of the strange foods which are important to different sections of mankind in other continents and climates." Thus is the aim of this book set out in the introduction and, on inspection, is found to be excellently fulfilled. Over 400 species are illustrated in colour and on the facing pages the origin, distribution and utilisation are concisely but fairly adequately described. The book concludes with short but informative essays on the domestication, dispersal and nutritional value of food plants. The botanist would, perhaps, like to see more species treated, especially from the tropics, rather than different varieties of apples and grapes, of which a necessarily very limited selection can be illustrated. The six pages devoted to algae, fungi and edible British wild plants could have been used more advantageously to provide, for example, an appendix of vernacular names.

As this is pre-eminently a picture book, special mention must be made of the colour reproductions. The register and delineation is good but the tones are, on the whole, highly unnatural although not altogether without a certain charm. South African readers will not recognise the brown pawpaws but the plates of *Rubus* and *Citrus* are most attractive.

This book was produced for the lay reader but it does have a place in S.A. botanical libraries, the users of which are not always familiar with tropical and north temperate food plants. It is very good value for 55/-.

A DICTIONARY OF THE ECONOMIC PRODUCTS OF THE MALAY PENINSULA by I. H. Burkill. 2 vols. with 3,684 pp. Kuala Lumpur, Malaysia: Ministry of Agriculture and Co-operatives, 1966 (2nd edition). £13.6.

Originally printed in a restricted edition, this work is now more freely available in a somewhat enlarged form. Regrettably a complete updating and revision, especially of the nomenclature, was not possible but nevertheless Burkill remains one of the standard encyclopedias of tropical plants and their utilisation. For South African readers it is an essential adjunct to Willis and Watt & Breyer-Brandwijk, a classic compendium of useless and useful information. Here the herbarium botanist will find excellent diversion from his newsprint drying papers and will be saddened to learn that "the Viceroy sent an expedition to the *Cinchona* regions; and in 1640 his wife, the Countess of Cinchon, returning to Europe, brought with her a quantity of the bark. The expedition of 1639 was described by the Jesuit, Christoval de Acuna, and is historical; but the return of the Countess is not, as her tomb at Cartagena testifies." He will doubtless be interested also to know that "Because the Portuguese had dubbed the tappers of *Hevea* 'squit makers' and called the tree 'syringe tree', Richard suggested Siphonia as a name for the genus. Schreber published it in 1791, well knowing that the tree had already the name *Hevea*, but fancying *Siphonia* as being more literary."

The work is well printed and, for a total of 3,684 pages, not really expensive.

A. R. A. NOEL

INSTRUCTIONS TO CONTRIBUTORS TO THE JOURNAL OF SOUTH AFRICAN BOTANY

This Journal provides a medium for the publication of the results of botanical research primarily on the flora of Southern Africa, whether systematic, morphological, ecological or otherwise and whether carried out in South Africa or elsewhere. Papers on botanical subjects of special interest and application in South Africa may be included.

Contributions must be original and should not be translations of previously published papers.

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Authors may be charged expenses for corrections if alterations are excessive.

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Papers should be type-written, double spaced throughout on one side of the paper and with margins of at least 3 cm (1 inch). Footnotes and elaborate tables should be avoided. Latin binomials should be underlined once to indicate italics. All other marking of copy should be left to the Editor. The original, plus at least one carbon copy, must be submitted.

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Each paper should be headed with a concise informative **title** in capitals with the author's name below. This should be followed by the name of the institution, where the work was carried out, underlined and placed within brackets.

A concisely written **abstract** in English and Afrikaans, of not more than 200 words, should precede the text.

The subject matter should be divided into sections under short appropriate **headings** such as: INTRODUCTION, MATERIAL AND METHODS, RESULTS, DISCUSSION, CONCLUSION, ACKNOWLEDGMENTS, etc.

Tables and **illustrations** should be on separate sheets. **Figures** and **graphs** should be in Indian ink on white card or Bristol board. Lettering for figures can be inserted by the printers in which case authors should indicate the desired lettering on the original figure lightly in pencil. The maximum dimensions available for figures are 18 cm $\times$ 12 cm (7″ $\times$ 4½″). Line drawings for blocks should be at least twice the size they will be when reduced for publication. All figures should be supplied with a scale. The most suitable method of indicating magnification is a scale line (in metric units) incorporated in the figure. Photographs for half-tone reproductions should be on glossy paper, clearly marked on the reverse side (in pencil) to indicate the top. Line drawings and half-tone illustrations are termed figures and should be numbered consecutively. Captions for figures should be typed on a separate sheet of paper.

TAXONOMIC PAPERS

Authors must adhere to the International Rules of Botanical Nomenclature. **Abbreviations** of **herbaria** must be cited in accordance with the most recent edition of Index Herbariorum, Pt 1 (The Herbaria of the World, 5th ed., 1964). When **new species** are described, the exact location of type material must be indicated. When proposing **new combinations** the full citation of the basionym is required. **Indented keys** with numbered couplets are preferred when dealing with a small number of taxa. **Bracket keys** should be used when dealing with a large number of taxa. When citing **synonyms** they should be arranged chronologically into groups of nomenclatural synonyms and these should be

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Bequaertiodendron magalismontanum (Sond.) Heine & J. H. Hemsley in Kew Bull. **1960**: 307 (1960).
Chrysophyllum magalismontanum Sond. in Linnaea **23**: 72 (1850). Type: Magaliesberg, *Zeyher*, 1849 (S, holo; BOL!, SAM!).
Zeyherella magalismontana (Sond.) Aubrév. & Pellegr. in Bull. Soc. bot. Fr. **105**: 37 (1958).
Pouteria magalismontana (Sond.) A. Meeuse in Bothalia **7**: 335 (1960).
Chrysophyllum argyrophyllum Hiern, Cat. Afr. Pl. Welw. **3**: 641 (1898). Syntypes: Angola, *Welwitsch* 4827, 4828, 4829 (BM!).
Boivinella argyrophylla (Hiern) Aubrév. & Pellegr. in Bull. Soc. bot. Fr. **105**: 37 (1958).
Chrysophyllum wilmsii Engl., Mon. Sapot. Afr.: 47 t. 16 (1904). Type: Transvaal *Wilms* 1812 (B†, holo.; K!).
Boivinella wilmsii (Engl.) Aubrév. & Pellegr. in Bull. Soc. bot. Fr. **105**: 37 (1958).

CITATION OF SPECIMENS

In the interests of uniformity contributors are requested to follow the recommendations of the Botanical Research Institute, Pretoria (Technical note: Gen. 4, Oct., 1967) by citing specimens according to the one degree grid system. Distribution data are given separately for each province and are arranged in the following sequences: South West Africa, Botswana, Transvaal, Orange Free State, Swaziland, Natal, Lesotho, Cape. Within each province degree squares are listed in numerical sequence, i.e., from west to east and from north to south. Whenever possible locality records should be given to within a quarter degree square. The collectors' names and numbers are underlined (printed in italics) to avoid confusion with the numbers of the degree squares, e.g.: NATAL—2829 (Harrismith): Cathedral Peak Forest Station (-CC), *Killick 1527* (PRE); . . . CAPE—3418 (Simonstown): Hottentots Holland mountains, Somerset Sneeukop (-BB), Nov., *Stokoe s.n.* sub. SAM *56390* (SAM).

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These should be given in the text as follows: Jones (1968) or (Jones, 1968) or, where reference to a specific page is required, Jones (1968:57) or (Jones, 1968:57). **Literature cited** should be arranged alphabetically by surnames, chronologically within each name, with suffixes a, b, etc., to the year for more than one paper by the same author in that year. Titles of **periodicals** must be abbreviated according to the *World List of Scientific Periodicals,* 4th ed., London: Butterworth or when unable to trace the title in this list (as will be the case in taxonomic papers where abbreviations of 18th and 19th century periodicals are required) the abbreviations given in *Botanico-Periodicum-Huntianum,* Pittsburgh: Hunt Botanical Library, 1968, should be followed. Periodical titles should be underlined once (for italics). If an author is unable to determine the correct abbreviation of a journal title he is advised to type it out in full and leave its abbreviation to the Editor. Titles of **books** should be underlined and given in full, together with the place of publication, name of the publisher and an indication of the edition if other than the first; e.g.:

Davis, P. H. and Heywood, V. H., 1963. *Principles of Angiosperm Taxonomy.* Edinburgh and London: Oliver and Boyd.

Riley, H. P., 1960. Chromosome numbers in the genus *Haworthia. Jl S. Afr. Bot.* **26**: 139—148.

Jl S. Afr. Bot. 37 (2): 75–102 (1971)

STUDIES IN THE GENUS *CERATIUM* SCHRANK, WITH REFERENCE TO SPECIMENS COLLECTED IN THE AGULHAS CURRENT, IN PARTICULAR FROM A LINE OF STATIONS OFF PORT ELIZABETH, DURING INTERNATIONAL GEOPHYSICAL YEAR 1958: 1

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Abstract

An historical review of the literature is given, followed by a taxonomic account of the Subgenus *Poroceratium* (Vanhöffen) Kofoid.

Uittreksel

STUDIES VAN DIE GENUS CERATIUM SCHRANK, MET VERWYSING NA MONSTERS WAT IN DIE AGULHASSEESTROOM VERSAMEL IS, VERAL VANAF 'N REEKS STASIES BUITE PORT ELIZABETH, GEDURENDE INTERNASIONALE GEOFISIESE JAAR 1958: 1.

'n Historiese oorsig van die literatuur word gegee asook taksonomiese verslag van die subgenus *Poroceratium* (Vanhöffen) Kofoid.

Introduction

Members of the genus *Ceratium*, are, with species of *Peridinium* Ehb., perhaps the most common of marine armoured dinoflagellates. Although many workers have studied *Ceratium*, the taxonomy is by no means completed, and cannot be, until cultural experiments determine the nature of variation; nor are many aspects of the biology fully understood.

The aim of the present account is to indicate the occurrence and degree of variation of the species in the Agulhas current, based on samples collected during I.G.Y. 1958. In these samples, routine investigations of the phytoplankton flora showed the armoured dinoflagellates to be much rarer than the diatoms. Accordingly, a more detailed examination was made of samples from the March and May cruises from the line of NGY stations off Port Elizabeth. (For data on the NGY stations see Zoutendyk 1960.)

Species of *Ceratium* in this area have been discussed or listed previously in general phytoplankton surveys: Karsten (1907), Taylor (1966), Nel (1968) and Thorrington-Smith (1969). A monograph of the genus from the Mozambique Channel has been published by Sournia (1967).

General Features of the Genus (See Fig. 1, A-F.)

The body is generally dorsiventrally compressed, and partly encircled by a transverse groove, the girdle, which divides it into an upper epitheca and a

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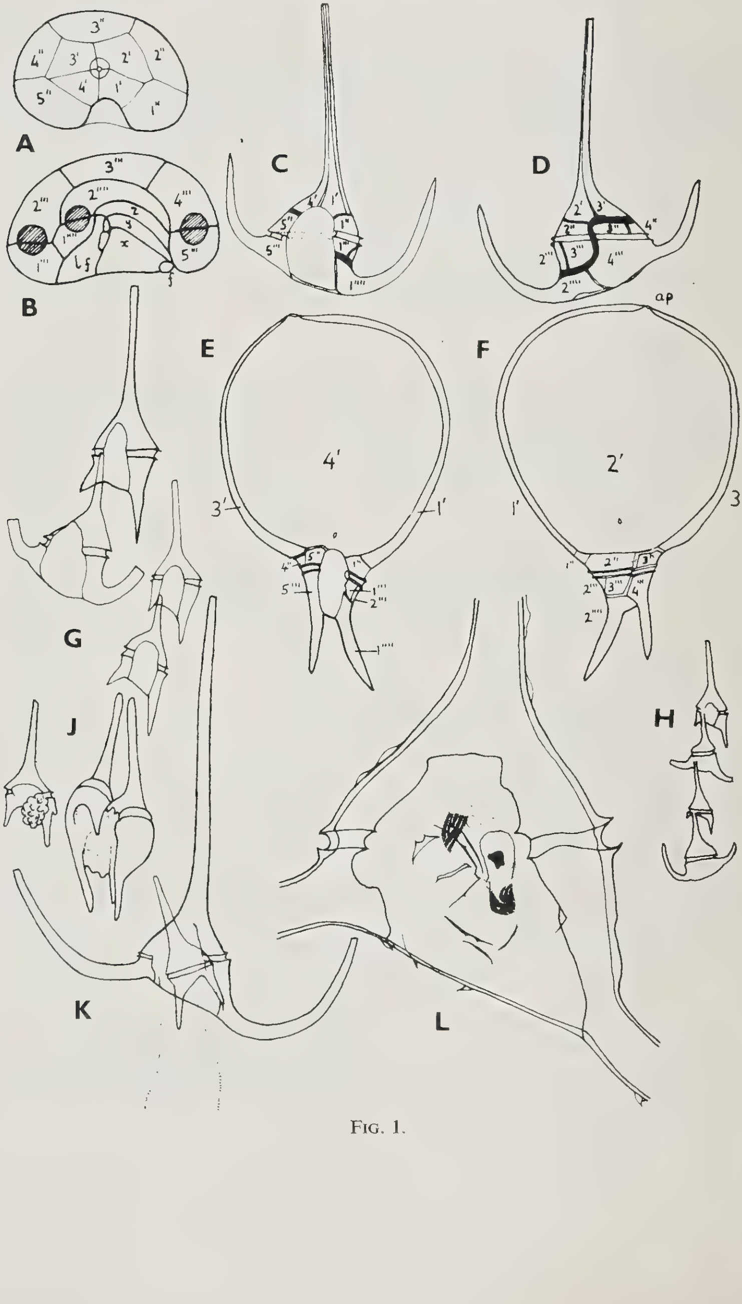

Fig. 1.

lower hypotheca. The ends of the girdle lie ventrally on either side of the ventral area. The posterior margin of the body is oblique, the acute inclination in relation to the girdle being towards the right side of the body. On the left side of the ventral area is a longitudinal furrow or sulcus, containing the flagellar pore, from which the transverse flagellum encircles the body in the depression of the girdle, and the longitudinal flagellum is backwardly directed to some distance beyond the posterior margin of the cell.

The plate formula appears to be constant throughout the genus, being 4′, 0a, 5″, 5‴, 2⁗, that is, the epitheca is composed of four apical plates and five precingulars and the hypotheca of five postcingular and two antapical plates. The girdle is made up of four plates, the ventral area of three plates and the sulcus of two.

The epitheca is generally drawn out into an apical horn of varying length, composed of the anterior parts of the four apical plates. The apex of the epitheca or the tip of the apical horn possesses an apical pore. In all marine ceratia two antapical horns project from the hypotheca. The left antapical horn is formed from the two antapical plates, the right horn from part of postcingulars four and five. In the freshwater *C. hirundinella* (Müller) Bergh, the hypotheca may possess up to five antapical horns. All horns are hollow, surrounding extensions of the protoplast.

In schizogony, all the apical plates, precingulars one and two and post-cingulars one to three, remain with the anterior daughter cell, while precingulars three to five, postcingulars four and five and both antapical plates are retained by the posterior daughter cell. Chains of cells arise due to adherence after schizogony. This tendency is more marked in some species than in others. The tip of the apical horn of the posterior cell rests ventrally on the right end of the girdle of the anterior cell. In the cells behind the front cell of a chain, the apical horn tends to be shorter, often markedly so.

Fig. 1. *A* and *B*, (Schiller 1937, original), showing plates of *C. hirundinella* (O.F.M.) Bergh: *A*, apical view, with apical horn and pore in centre; *B*, antapical view, with three antapical horns; 1′–4′ = apical plates, 1″–5″ = precingular plates, 1‴–5‴ = postcingular plates, 1⁗, 2⁗ = antapical plates, *x*, *y*, *z* = plates of ventral area, *lf* = sulcus, *f* = depression into which fits the apical horn of the posterior member of a chain; *C* and *D*, (Schiller 1937, after Jörgensen), showing plates of *C. tripos* (O.F.M.) Nitzsch: *C*, ventral view; *D*, dorsal view; the heavy line indicates division of plates during schizogony; *E* and *F*, (Kofoid 1907b), showing plates of *C. gravidum* Gourret: *E*, ventral view; *F*, dorsal view; *G*, (Lohmann 1908), "Temporalvariationen von *C. tripos balticum* . . . forma *lineata* . . . forma *truncata*", fragments of heteromorphic chains of *C. tripos; H*, the same, (after Tschirn 1920, fide von Stosch 1964); *J*, (after Entz 1924, fide Hall 1925), "coupling" in *C. hirundinella; K* and *L*, (von Stosch 1964), conjugation in *C. horridum* Gran: *K*, early stage; *L*, later stage, with fragments of thecal plates from the male gamete in the ventral area, the two nuclei lying adjacent to one another.

The epithecal plates are porulate and may be ornamented with a series of ridges in a linear to a reticulate pattern. The rims of the girdle are expanded into narrow membranous blade-like projections or lists and a list borders the left side of the sulcus. Lists, associated with the sutures between the relevant thecal plates, may occur at the base of the hypotheca, sometimes extending onto the adjacent part of the antapical horns, or on either side of the base of the apical horn, extending onto the epitheca; these lists, with smooth to serrated to denticulate margins, may be supported by spines. The thecal wall may be thickened along the sutures between plates, in particular along the sutures at the base of the hypotheca, and on one or both sides of the proximal parts of the apical and antapical horns.

An Historical Account of the Literature dealing with various Aspects of the Genus.

General: The genus *Ceratium* was established by Schrank in 1793, the name being derived from the Greek for "small horn." The original description was somewhat inadequate: "Vermis inconspicuus amorphous rigidulus, corniculis circumferentiae pluribus." Schrank described two species, *C. pleuroceras* and *C. tetraceras*, which appear to belong to the polymorphic freshwater species, *C. hirundinella* (Müller) Bergh. As *Bursaria hirundinella* Müller (1773), this was the first species of *Ceratium* to be described. The first marine *Ceratium* to be described was *C. tripos* (Müller) Nitzsch (1817), as *Cercaria tripos* Müller (1776).

Several species of *Ceratium* were described during the period 1833–1873 as members of his genus *Peridinium* (1832), by the great microscopist Ehrenberg. Claparède & Lachmann (1858–1859) distinguished *Ceratium* from *Peridinium* on the basis of the horns. Stein (1883) was the first to realise that the composition of the thecal plates was the most satisfactory basis for the classification of the armoured Dinoflagellates, and accordingly differentiated between *Ceratium* and *Peridinium* (l.c.: 11), but did not establish the complete plate formula for *Ceratium*. Kofoid (1907b) showed the plate formula to be the same for all the ceratia he examined. He described the epitheca as having four precingular plates, but Jörgensen (1911) found the number to be five.

In the latter part of the nineteenth century, references to new species of *Ceratium* are either found in general works on Peridinians, sometimes not formally described, or in accounts of marine phytoplankton from different localities. The first work of this nature to deal with *Ceratium* extensively is Gourret's "Sur les Péridiniens du Golfe de Marseille" (1883).

The species concept in *Ceratium* was at first somewhat confused. Forms with distinctive shapes such as *C. gravidum* Gourret (1883) were recognised as distinct species; not so forms in which the antapical horns were directed anteriorly, or those with triangular epithecae and backwardly directed antapicals.

Some writers such as Bergh (1882) referred to the former as the "Formenkreis des *C. tripos*" and to the latter as the "Formenkreis des *C. furca*."

Following Hensen's pioneer work on plankton (1887), the numbers of phytoplanktologists increased, stimulated by the realisation of the relationship between plankton and fishing and the organisation of oceanographic expeditions to all parts of the globe. The first large expedition, in the phytoplankton reports of which *Ceratium* is mentioned, was Hensen's Plankton Expedition of 1889 (Schütt 1892, 1895). A comprehensive series of illustrations of ceratia were published by Karsten (1905, 1907) in his account of the phytoplankton collected during the world-wide deep-sea Valdivia Expedition.

The first major monograph on *Ceratium* was that of Jörgensen (1911), which included detailed accounts of all the known species. This was followed by his work on the Mediterranean ceratia (1920), in which emphasis was placed on hydrological conditions and seasonal distribution, as Jörgensen wished to determine transportation of species from the Atlantic. A number of new taxa were included, sometimes without formal descriptions, and Jörgensen used the terms form and variety indiscriminately for the same taxon, occasionally giving new epithets to the typical infraspecific taxa of some species.

Many regional accounts of *Ceratium* followed, of which a few are mentioned below. Some dealt solely with the taxonomy of the species, others with the distribution of ceratia related to environmental conditions. Böhm (1931, Northern and Western Pacific) showed the range of variation in some species by a series of measurements and illustrations. Peters (1932, South Atlantic) and Steemann Nielsen (1934, South Pacific) considered the factors, in particular temperature, affecting both distribution and infraspecific variation. Peters considered distribution a criterion for the recognition of some problematic subspecific taxa. Steemann Nielsen included tables of measurements illustrating some aspects of infraspecific variation. Graham & Bronikowsky (1944, Pacific and North Atlantic) examined many hundreds of specimens and gave a comprehensive series of illustrations of infraspecific variation, with a most detailed account of distribution and associated hydrological factors, but unfortunately they included few measurements of specimens.

The next general taxonomic treatment of *Ceratium* was published by Schiller (1937) in Rabenhorst's Kryptogamenflora, and it is probably the basic reference for *Ceratium* most used by subsequent workers. There are, however, a number of errors in the bibliography and some of the subspecific categories are cited inaccurately.

Two postwar regional accounts of *Ceratium* are by Wood, in his studies of the Dinoflagellates of the Australian Region (1954, 1963), and Sournia (1967). Sournia's work on ceratia of the Mozambique Channel includes a useful comprehensive bibliography and a new unconventional approach to the treat-

ment of some subspecific taxa. Sournia writes "... in the case of species which have a continuous sequence of morphological variations apparently related to temperature ... to keep only to the name of the species ... would ... bury the problem ... the usage of infraspecific taxa would ... be multiplied by infinity." Pointing out that the genetic basis of variation is unknown, Sournia proposed that the rank "form" be applied to cases of variation not related to temperature, while infraspecific thermophylic and psychrophylic taxa should be classed as "varieties", with the cases with intermediate temperature preference given an epithet "outside the classical taxonomy", indicating the proximity to one or other of the varieties, e.g. "*C. horridum* (Cl.) Gran *horridum*>*buceros*."

Biometric methods of assessment of variation in taxa of *Ceratium* have been used by Lopez (1955, 1966) and Yarranton (1967). Lopez used measurements of antapical horn length and girdle diameter to analyse seasonal variations and relationships in members of the *C. tripos* complex and the Subgenus *Ceratium*. Yarranton showed that the determination of the coefficients of the curves of the three horns could be used as a basis of classification in the four taxa he studied.

The first major work on the cytology of *Ceratium* was that of Hall (1925) on mitosis in *C. hirundinella*, which includes a good account of earlier research. Later accounts are that of Skoczylas (1958) on mitosis in *C. cornutum* (Ehb.) Cl. & Lach., a general account of chromosome structure in the Dinophyceae by Dodge (1966) and the work of Jahn et al (1963) on the movement of ceratium flagella.

Cultural experiments on species of *Ceratium* have been carried out by Hasle and Nordli (1951) and Nordli (1957), and Nielsen (1956) has investigated factors causing variation in certain ceratia in their marine environment.

Chain formation, polymorphy and sexual reproduction: (See Fig. 1, G–L.)

The formations of chains of normal individuals of ceratia of similar size, with slight variation in disposition of antapical horns and apical horn length was recorded as early as 1830 by Michaelis, (*fide* Kofoid 1909). Kofoid noted that in a complete chain arising by normal vegetative division, the epitheca of the anterior member and the hypotheca of the posterior member are derived originally from the same cell.

Polymorphy in species of *Ceratium* was recognised by early writers such as Bergh (1882) and Hensen (1887), although their interpretation was incorrect. Hensen found small cells about one eighth to one tenth the size of normal *C. tripos* cells, with short backwardly or slightly laterally directed antapical horns. The former he considered were young forms of *C. furca* (Ehb.) Cl. & Lach, the latter young *C. tripos*. Lohmann (1908) was the first to discover typical *C. tripos* cells in chains together with similar sized or very slightly smaller

heteromorphic cells, and in the same samples, a series of forms ranging from the small cells recorded by Hensen to normal *C. tripos* of normal size. He did not state specifically that he had found chains showing a continuous sequence from the very small heteromorphic cells to normal *C. tripos*, but wrote: "An dieser Ketten liess sich nun leich der Nachweiss führen, dass alle Jugendformen Hensens besondere Formen von *C. tripos balticum* sind . . ." He regarded these as "seasonal temporary variations" and suggested that the very small forms might conjugate.

Kofoid (1909), who found a chain of three heteromorphic *C. tripos* cells of similar size, suggested that Lohmann's small forms might be independent species unrelated to *C. tripos*. He considered the heteromorphic forms he found to be "mutants", arising due to environmental changes, in the course of asexual reproduction. Tschirn (1920, fide von Stosch 1964) illustrated a chain including a normal *C. tripos* and a heteromorphic form, smaller in size, due, it was suggested, to "depauperising division". Jörgensen (1920) encountered some single heteromorphic forms, similar to those found by Lohmann, which were "relatively frequent in the region (of the Mediterranean) of the fresher water from the Black Sea." He considered these to be "due to a degeneration, caused by certain hydrographical conditions," such as a variation in salinity.

In culture, a range of forms, not in chains, from small heteromorphic cells to normal *C. tripos* cells, was found by Hasle and Nordli (1951), and very small heteromorphic cells were found in a single cell culture of *C. horridum* (Cl.) Gran by von Stosch (1964). Von Stosch suggested that the end products of a differentiation series from a normal cell could not, by division, revert back to normal cells while the intermediates could.

Abnormal forms with extra horns were found both in culture and in nature by Hasle and Nordli.

The literature indicates that these heteromorphs and abnormally horned cells occur rarely in marine species, while very small heteromorphs have not been observed in freshwater species.

In the freshwater *C. hirundinella*, the number of antapical horns normally varies from one to three, sometimes up to five, (Kofoid 1907).

Sexual reproduction in a marine species: von Stosch (1964) observed a single instance of conjugation in a single cell culture of *C. horridum*, between a normal cell and a small heteromorph, the latter having been produced in the clone subsequent to its inception. The ventral areas of the two cells touched and the contents of the small cell rounded off and passed into the large cell. A later stage showed the plates of the presumed male gametophyte disintegrated in the region of the two nuclei which lay adjacent to one another. Von Stosch suggested that the thecal plates could have been "partially reabsorbed." Incipient fusion

of the nuclei was observed but subsequent development is unknown.

Apstein (1910, fide von Stosch) reported a process of budding in *C. tripos*, where a small cell, similar to one of Lohmann's heteromorphs was observed budding off from the ventral area of a normal *C. tripos*. The later observations of von Stosch suggest that this could have been a misinterpretation of an instance of conjugation in *C. tripos*.

Encystment and sexual reproduction in freshwater species: Encystment in marine species has not been reported, but in freshwater ceratia encystment is known to occur, the cyst developing inside the theca of a normal shaped cell. A naked Gymnodinium-like swarmer, the Praeceratium stage, is liberated, which develops a theca (Schiller 1937). This divides into four daughter cells, which develop into normal adults, two of which inherit respectively the hypo- and epi- theca of the Praeceratium wall, (von Stosch 1965).

The actual division has not been observed, but von Stosch's observations (1964) on the configuration of the chromosomes of the Praeceratium nucleus, referred to as the "Knäuelstadium," indicate that it is a meiotic division. Following research on mitosis in *C. cornutum* by Skoczylas (1958) who found no stage resembling the "Knäuelstadium" during mitosis, von Stosch found that the chromosomes of the "Knäuelstadium" had the configuration typical of the post-zygotene stage of meiosis. According to von Stosch, a "Knäuelstadium" has been observed in certain marine ceratia of normal shape.

What was generally considered to be conjugation in *C. hirundinella* was first observed by Zederbauer (1904) and later by Entz (1924, fide Hall 1925), who described the joining together of two cells by a protoplasmic bridge. Actual nuclear migration was not observed, but the occurrence at the same time of numerous cysts was considered indicative that conjugation had taken place. Later Entz, (1930, fide von Stosch 1964), showed the apparent conjugation bridge to be an artefact. It is of interest to note that Paulsen (1909) observed specimens of the marine *C. lineatum* (Ehb.) Cl. with sacs with granular contents attached ventrally in the region of the flagellar pore, such as observed by Zederbauer in cells of *C. hirundinella* before "conjugation".

Von Stosch (1965) commenting on sexuality in *C. cornutum* wrote: "Der Sexualprozess, der direkt noch nicht beobachtet werden konnte, ist mit grösster Wahrscheinlichkeit heterogam." He observed in clones of *C. cornutum* the development of cells which differed from normal cells in size, being thinner, and in plastids and pigment content. These he termed "Mikroschwärmer." Later, binucleate cells were seen in the clone, with fragments of thecal plates on the ventral side, indicating that a process had occurred similar to the conjugation observed in *C. horridum*. These putative zygotes remained motile for a long time during which nuclear fusion took place. Later the protoplasmic

cell contents rounded off, withdrawing from the horns, and a cyst membrane was formed within the thecal wall of the zygote.

Exuviation, Autotomy and regeneration: Kofoid (1908) observed specimens in which shedding or exuviation of certain thecal plates had occurred, and suggested that this could be an "adaptation to changed conditions of flotation". He also observed that many long horned ceratia had broken horns, and actually found cells with apparent abscission zones in the walls of as yet unbroken horns, and cells in which the theca surrounding the horn had broken off, leaving the protoplast surrounded by a uniformly thin layer, "impregnated with wall material?" extended horn-like beyond this. This was seen even in cells with almost the entire horn theca broken off. Kofoid concluded that regeneration of broken horns took place and that shedding of the horns was not necessarily accidental, and termed the active process of horn shedding autotomy. This he considered to be likewise a flotation adjustor.

Distribution and ecology: The work of Peters (1932) and Steemann Nielsen (1934) and Graham and Bronikowsky (1944) has been mentioned. Graham (1941) summarised his investigations of factors affecting the distribution of ceratia in the Pacific and North Atlantic with reference to the observations and conclusions of Peters and Steemann Nielsen. Graham found that variations in salinity did not appear to affect species distribution, while a geographic classification of the species could be made on the basis of temperature. Only three categories could be recognised, "cosmopolitan," "tropical" and "sub-polar," with no evidence of truly temperate species, the temperate latitudes being populated by tropical and cosmopolitan forms and occasionally sub-polar ceratia. Tropical species could be subdivided further according to the ranges of temperature at which they occurred, into "intolerant," with surface temperatures never less than 19°C, "slightly tolerant", "tolerant" and "very tolerant". Graham pointed out that currents could displace certain species from their "normal" temperature range. He further found that some ceratia increased in frequency from the surface to a depth of 100 meters, and, following Steemann Nielsen, classified them as "shade species".

Subdivisions of the Genus

Vanhöffen (1896) divided *Ceratium* into four separate genera: *Ceratium* for species in which the antapical horns were directed forwards as in *C. tripos*; *Biceratium* for species in which the antapicals were not very dissimilar in length and directed backwards, as in *C. furca* (Ehb.) Clap. & Lach.; *Amphiceratium* for species with backwardly directed antapicals of very unequal length as in

C. fusus (Ehb.) Duj., and *Poroceratium* for species in which the epitheca was inflated laterally and lacked an apical horn, as in *C. gravidum* Gourret.

Gran (1902) treated the taxa *Amphiceratium* and *Biceratium* as Sections of the genus *Ceratium*, and proposed the name *Euceratium* for the Section containing species like *C. tripos*. As he was only dealing with plankton from Norwegian waters, he did not encounter members of the *Poroceratium* group.

Ostenfeld (1903) changed Gran's Sections to Subgenera and divided Subgenus *Euceratium* (Gran) Ostf. into two Sections: *Tripos* Ostf. and *Macroceros* Ostf., the former composed of species with the antapical horns closed at the distal end and horn lists without spines, the latter incorporating species with antapical horns open at the distal ends and spiny lists.

Karsten (1905, 1907) used his own classification. He placed all species with recurved or forwardly directed horns in "Subgenus *Ceratium tripos*" and used a trinomial system of nomenclature for these species e.g. "*C. tripos azoricum* Cl." Karsten (1907) divided this Subgenus into two Sections, *Protuberantia* in which the antapicals were initially backwardly directed and then recurved anteriorly and *Rotunda* in which the antapicals were forwardly directed from their inception. In part, these correspond to the Sections of Ostenfeld, but included in Section *Rotunda* was "*C. tripos platycorne*" (Daday) Karsten with spiny horn lists. Species belonging to the Subgenera *Amphiceratium* and *Biceratium* were treated as varieties of *C. furca*.

Kofoid's demonstration of the uniformity of thecal structure in species of *Ceratium* (1907b) supported the reincorporation of Vanhöffen's genera into a single genus. In 1909 Kofoid established the Subgenus *Poroceratium* (Vanhöffen) Kof. and divided Subgenus *Euceratium* (Gran) Ostf. into two Subgenera: *Tripoceratium* with rounded posterior margin and closed antapical horn tips, and *Macroceratium* with the characters of Section *Protuberantia* Karsten, and the tips of the antapical horns "truncate, open or contracted or rounded, but usually with terminal pore".

Jörgensen (1911) retained as Subgenera *Poroceratium*, *Biceratium*, *Amphiceratium* and *Euceratium*, dividing the last three into a number of Sections based upon horn and body characters: Subgenus *Biceratium*, Sections *Digitata* Jörg., *Lanceolata* Jörg., *Cornuta* Jörg., *Candelabra* Jörg. and *Furciformia* Jörg.; Subgenus *Amphiceratium*, Sections *Inflata* Jörg. and *Fusiformia* Jörg., and Subgenus *Euceratium*, Sections *Dens* Jörg., *Tripos* Ostf., *Limulus* Jörg., *Platycornia* Jörg., *Palmata* Jörg., *Macroceros* Ostf., and *Reflexa* Jörg.

In 1920, Jörgensen established a new Subgenus *Archaeceratium* incorporating Section *Digitata* Jörg. and Section *Poroceratium* (Vanhöffen) Jörg., and in Subgenus *Biceratium*, separated as Section *Pentagona* Jörg., *C. pentagonum* Gourret and its allies from Section *Furciformia*. Schiller (1937) followed this treatment, transferring Section *Lanceolata* Jörg. to Subgenus *Archaeceratium*.

Sournia (1967) also followed this classification, omitting Sections *Digitata* and *Lanceolata*, as he did not find the constituent species in his samples. As the type species of *Ceratium*, *C. hirundinella* (Müller) Bergh, was in the Subgenus *Biceratium* (Vanhöffen) Kof., Sournia replaced this name with Subgenus *Ceratium* (Article 22 of the International Code, Lanjouw 1966), and substituted Subgenus *Orthoceratium* Sournia for Subgenus *Euceratium* (Gran) Ostf., (Article 21).

Jörgensen (1920) distinguished Subgenus *Archaeceratium* from the other Subgenera on the nature of the apical plates of the epitheca. The nature of the apical plates has not, however, been recorded for all species of *Ceratium*.

These subdivisions of the genus are only applicable to the commonly occurring, so-called normal forms of *Ceratium*, for the backwardly directed horns of the small heteromorphic forms of *C. tripos* and *C. horridum*, members of the Subgenus *Orthoceratium*, are characteristic of the Subgenus *Ceratium*. Indeed, some authors have confused *C. lineatum* (Ehb.) Cl. belonging to this Subgenus with small heteromorphs of *C. tripos*, e.g. Paulsen (1908).

With the above reservations, Jörgensen's subdivision of *Ceratium* into Subgenera and Sections, with the alterations of Schiller and Sournia, is adopted in the following account.

Characters of the Subgenera

Subgenus **Poroceratium** (Vanhöffen) Kofoid.

The epitheca lacks an apical horn and apical plates four and two are greatly enlarged, composing most of the ventral and dorsal sides of the epitheca. Apical plates one and three are lateral, very narrow and boat-shaped. The antapical horns are posteriorly directed, only in *C. digitatum* Schütt, is the left antapical horn recurved anteriorly. The right antapical horn is never less than one quarter of the length of the left. All are marine species.

In the three remaining subgenera, in all the species examined, the four apical plates are of similar size, two on the ventral and two on the dorsal side of the epitheca, with apical plates one and four both in contact with the ventral area.

Subgenus **Ceratium.**

The apical horn is indistinctly to distinctly differentiated from the epitheca. The antapical horns are posteriorly directed, the right horn never less than one fifth of the length of the left horn. In freshwater species the antapicals vary in number from one to three, occasionally up to five. The only subgenus with both freshwater and marine species.

Subgenus **Amphiceratium** (Vanhöffen) Ostenfeld.

The apical horn is indistinctly to distinctly differentiated from the epitheca.

The cells, including the horns, are long and slender and the body is not very compressed. Both antapical horns are posteriorly directed, the right horn never exceeding one fifth of the length of the left horn, often it is much shorter, sometimes rudimentary or absent. Marine species.

Subgenus **Orthoceratium** Sournia.

The apical horn is distinctly differentiated from the epitheca. Both antapical horns are either anteriorly directed from their inception, or at first posteriorly directed and then recurved forward, except in *C. reflexum* Cl., where only the right horn is anteriorly directed. With two exceptions both horns are more or less similar in length. Marine species.

Subgenus **Poroceratium** (Vanhöffen) Kofoid (1909): 219.

Gen. *Poroceratium* Vanhöffen (1896): 133.

Subgen. *Archaeceratium* Jörgensen (1920): 6.

Diagnosis: Differs from the other subgenera in the nature of the apical plates. Apicals four and two are greatly enlarged composing respectively most of the ventral and dorsal sides of the epitheca, while apicals one and three are lateral, very narrow and boat-shaped.

The name is derived from the ring pore present in the epitheca of some of the species. Because the Subgenus had been enlarged to include species lacking a ring pore, Jörgensen (1920) changed its name to Archaeceratium.

According to Jörgensen (1911), the ring pore is a ring-shaped structure which is mounted on the inside of apical plates two and four, joining them tightly together, and allowing the protoplast no access to the inside of this ring. Kofoid (1907) described the pore as perforating the epitheca, which is not necessarily implied by Jörgensen. Kofoid also noted that the degree of development of the ring pore was subject to variation, "even to its suppression" in *C. gravidum* Gourret, the type species of Vanhöffen's genus. No later work seems to have been done on this structure. Graham & Bronikowsy's figures (1944) of *C. gravidum* include some specimens lacking a ring pore, while Wood (1963b) showed ring pores in figures of *C. praelongum* (Lemm.) Kof. and *C. digitatum* Schütt, both of which, according to other authors, lack a ring pore.

In *C. lanceolatum* Kof. and *C. gravidum*, the only apical plate to adjoin the ventral area is apical four, while in *C. praelongum* a small part of apical one also touches the ventral area. (See Fig. 2, D,E.) There is no indication in the literature of the relationship between the ventral area and the apical plates in the other species.

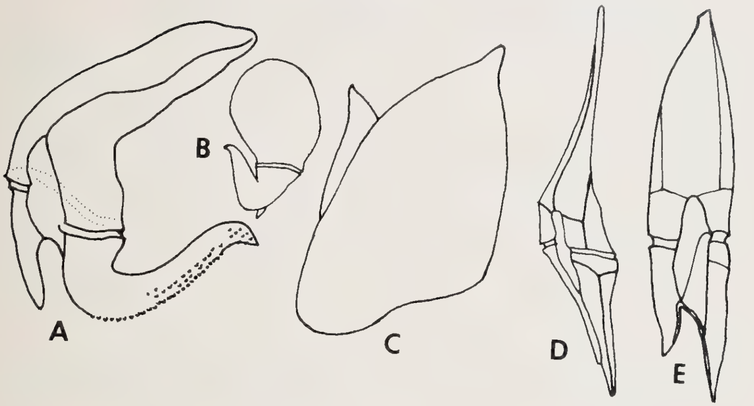

FIG. 2.

Fig. 2. *A* and *C*, (Schütt 1895), *C. digitatum: A*, latero-ventral view; *C*, ventral view of upper part of epitheca; *B*, (Peters 1932), "*C. digitatum var.*": dorsal view; *D*, (Graham & Bronikowsky 1944), *C. praelongum:* latero-ventral view; *E*, (after Kofoid 1907a), *C. lanceolatum:* ventral view.

Kofoid (1907b) numbered the large apical plates of this Subgenus as apical one, on the ventral side, and apical three, on the dorsal side, but Jörgensen (1911) considered them to be apicals four and two respectively. Jörgensen's numbering is adopted because in the other subgenera, both apicals four and one adjoin the ventral area, more or less equally, and in *C. praelongum*, the narrower of the two apicals adjoining the ventral area lies to the *left* of the much broader apical, and may be considered as apical one, with the inference that in *C. gravidum* and *C. lanceolatum*, apical one has been so displaced by the enlarged apical four that it no longer adjoins the ventral area.

KEY TO SECTIONS AND SPECIES.

I. Body slightly dorsiventrally compressed; epitheca dorsiventrally convex-concave or involuted forming longitudinal folds; left antapical horn markedly dorsally or dorsolaterally curved, spinulate.
Section *Digitata*.

II. Body markedly dorsiventrally compressed; epitheca flat and blade-like above ventral area; left horn never markedly curved as above, smooth.
i. Epitheca in full dorsal or ventral aspect expanded laterally, apex rounded.
Section *Poroceratium*.
ii. Epitheca in full dorsal or ventral aspect lanceolate, apex a truncated point.
Section *Lanceolata*.
C. lanceolatum.

Section **Poroceratium.**

1) Lateral expansion of epitheca gradual, ring pore apparently always absent.
C. praelongum.

2) Lateral expansion of epitheca at base of apical plates fairly abrupt.
   A. Epitheca never broader than long, ring pore generally present. *C. gravidum.*
   B. Epitheca broader than long, ring pore always present. *C. cephalotum.*

Section **Digitata.**

1) Epitheca involuted to form longitudinal folds, tip of epitheca constricted to form a very short ill-defined apical horn, length of epitheca exceeding 190μ. *C. schroeteri.*
2) Epitheca dorsiventrally convex-concave, length of epitheca not exceeding 120μ. *C. digitatum.*
   A. Left antapical horn dorsally recurved so that its tip lies almost level with, to anterior to, girdle; apex of epitheca bluntly acuminate-cuspidate. *C. digitatum* subsp. *digitatum.*
   B. Left antapical horn dorsally recurved so that its tip lies some distance posterior to the girdle; apex of epitheca rounded. *C. digitatum* subsp. *rotundatum.*

Section **Poroceratium.**

Diagnosis: Differs from the other Sections in the rounded apex of the epitheca and in the marked dorsiventral compression of the body, particularly in the epitheca above the ventral area.

Jörgensen (1920) apparently intended to divide this Section into two Subsections, based upon the occurrence of the ring pore, but described only one Subsection, Annulifera, containing *C. gravidum* and presumably *C. cephalotum* (Lemm.) Jörg. The latter species and *C. praelongum*, which he considered transitional between Sections *Digitata* and *Poroceratium*, were absent from his Mediterranean samples. As the ring pore may be absent in *C. gravidum*, this subdivision seems inadvisable until the relationship between the apical plates and the ventral area is established in *C. cephalotum.*

Ceratium gravidum Gourret (1883): 58, pl. 1, fig. 15.
Schütt (1895) Pl. 11, fig. 41, 1–5; Vanhöffen (1896): 133; Okamura & Nishikawa (1904): 127, pl. 6, fig. 21; Kofoid (1907b): 182, figs. 7, 8; Jörgensen (1911): 10, pl. 1, fig. 8; (1920): 8; Forti (1921): 31, pl. 1, fig. 12, 13; Böhm (1931a): 351; Peters (1932): 28, pl. 2, fig. 12g; Steemann Nielsen (1934): 8, figs. 3, 4; (1939): 6; Schiller (1937): 357, fig. 389; Schubert (1937): 382; Graham & Bronikowsky (1944): 15, figs. 3 A–N, 4 P–U; Wood (1954): 272, fig. 186 a–c; Silva (1955): 155, pl. 7, fig. 1; Halim (1960) Pl. 4, fig. 21; Taylor* (1966): 463; Sournia (1967): 388, pl. 1, fig. 3.

Poroceratium gravidum Vanhöffen (1897): 382, pl. 5, fig. 12.
C. gravidum var. *angustum* Jörgensen (1911): 10, pl. 1, fig. 11.
C. gravidum var. *latum* Jörgensen (1911): 10, pl. 2, fig. 12; Forti (1921): 32, pl. 1, fig. 13.

* Given in check-list.

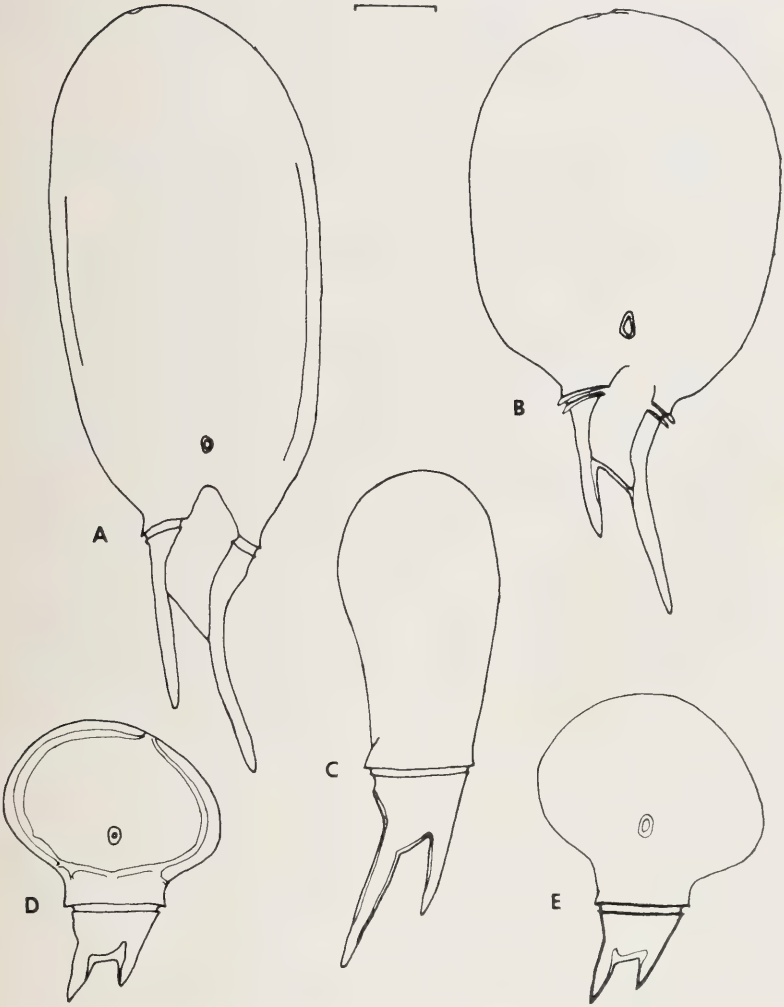

FIG. 3.

Fig. 3. *A* and *B*, *C. gravidum* in ventral view, apical pore and ring pore shown; in *B*, thecal wall shown in optical section at base of hypotheca and inner side of right antapical horn; *C*, *C. praelongum*, dorsal view; *D* and *E*, *C. cephalotum* in dorsal view; in *D*, sutures between epithecal plates partly discernible. Camera lucida drawings of specimens from stations in the Agulhas current. (The scale line indicates 50μ.)

C. gravidum var. *elegans* Jörgensen (1920): 10.
C. gravidum f. *obovatum* Jörgensen (1920): 8, fig. 4.
C. gravidum var. *elongata* Wood (1963b): 40, fig. 146.
C. oviformis Daday (1888): 102, pl. 3, figs. 7, 9.

Description: The mid body is dorsiventrally compressed, the compression becoming very pronounced above the ventral area, so that the part of the epitheca composed of the apical plates is flattened and blade-like. Seen in full ventral aspect, the *epitheca* is more or less obovate, the epithecal width varying from half to three quarters of the epithecal length; above the girdle, in the region of the precingular plates, there is only a slight increase in width relative to the girdle, then at the base of the apical plates the epitheca expands laterally fairly abruptly, less so in narrow forms, and sometimes slightly more on the right than on the left side; further lateral expansion is very gradual, maximum width being reached at half to two thirds of the length of the epitheca above the girdle; the apex is rounded, the apical pore displaced a little to the right; the ring pore, which may be absent, is situated medially in the lower half of the epitheca; the *hypotheca* tapers slightly to an oblique base. The *antapical horns* are parallel or slightly divergent, directed posteriorly or a little to the left, the left horn may be very slightly curved; the wall thickness and width of the horns varies and the right horn is generally half, sometimes three quarters of the length of the left. (See Fig. 3, A, B.)
Dimensions: In specimens examined: In full ventral aspect, girdle diameter 54–66μ; length epitheca 207–282μ; maximum width epitheca 144–198μ; length left horn 60–90μ; length left profile of hypotheca from base of horn to girdle about 42μ. *From literature:* Daday (1888), length epitheca 75–90μ; maximum width epitheca 70–75μ; length left horn from girdle 45μ; Jörgensen (1911), diameter 60–70μ; length epitheca 200–300μ.
Distribution: A widespread, but never abundant, shade species in tropical, subtropical and occasionally temperate waters. (See Table 1).

A subdivision of this species is unnecessary. Jörgensen's varieties were founded on variations in the shape of the epitheca due to differences in the width relative to the length. Peters (1932) considered these subdivisions superfluous on the grounds of their similar distribution. Graham and Bronikowsky (1944), after examining hundreds of specimens came to the conclusion that there was no discontinuity in the range of variation of forms, and gave a convincing series of illustrations, but no measurements.

Ceratium cephalotum (Lemmermann) Jörgensen (1911): 10, pl. 1, fig. 10.

Böhm (1931b): 43; Peters (1932): 28; Steemann Nielsen (1934): 7, fig. 2; (1939): 6; Schiller (1937): 356, fig. 388; Schubert (1937): 382; Graham &

Bronikowsky (1944): 15, figs. 2 A–C; Wood (1954): 271, fig. 185; Taylor* (1966) 462; Sournia (1967): 388, pl. 1, fig. 2; Nel* (1967): 98.

C. gravidum var. cephalotum Lemmerman (1900): 349, pl. 1, fig. 16; Karsten (1907): 415, pl. 50, fig. 1 a, b.

C. gravidum var. hydrocephala Schröder (1906): 369, fig. 44.

"Typenkreise der Gattung Ceratium" Schütt (1892): 269, fig. 79, 10a.

Description: The *epitheca* is dorsiventrally compressed and expanded laterally as in *C. gravidum;* seen in full ventral aspect, maximum epithecal width occurs at about mid epithecal length and is slightly more than, to one and a half times the epithecal length; the ring pore is apparently always present, approximately in the centre of the epitheca. The *antapical horns* are short and straight, the right horn about half the length of the left. (See Fig. 3, D, E.)
Dimensions: In specimens examined: In full ventral aspect, girdle diameter 45–48μ; length epitheca 111–114μ; maximum width epitheca 120–132μ; length left horn 27μ; length left profile of hypotheca from base of horn to girdle 27μ. *From literature:* Diameter 55μ; length epitheca 109–130μ; maximum width epitheca 157–170μ; length left horn 27μ.
Distribution: A rare species found in warm waters of all the oceans; not recorded from the Mediterranean. Graham and Bronikowsky describe it as a rare intolerant tropical shade species. (See Table 1).

There is some variation in the width of the epitheca, in particular with regard to the lateral expansion on the left side, but a subdivision of the species is superfluous. The variety described by Schröder is a specimen with a very broad epitheca.

Ceratium praelongum (Lemmermann) Kofoid ex Jörgensen (1911): 9, pl. 1, fig. 9; Kofoid (1907b): 182.

Paulsen (1930): 75, fig. 45; Böhm (1931b): 43, fig. 37a; Peters (1932): 28, pl. 2, fig. 12 f; Steemann Nielsen (1934): 7, fig. 1; (1939): 6; Schiller (1937); 356, fig. 387; Schubert (1937): 382; Graham & Bronikowsky (1944): 14, figs. 1 A–D; Silva (1957): 58, pl. 3, fig. 4; Wood (1963b): 40, fig. 148a, ?148b; Taylor* (1966): 463; Sournia (1967): 386, pl. 1, fig. 1.

C. gravidum var. praelongum Lemmermann (1900): 349, pl. 1, fig. 15; Ostenfeld & Schmidt (1901): 164; Karsten (1905b): 148; (1907): 415, pl. 50, fig. 2a, b.

The combination *Ceratium praelongum* was first used by Kofoid (1907) in a comment on the occurrence of the ring pore, which is apparently never

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* Given in check-list.

present in this species. Wood's figure (1963, 148b) showing a specimen with a ring pore in the upper third of the epitheca is dubious.

Description: The *epitheca* is compressed as in *C. gravidum;* seen in full ventral aspect, there is a very gradual lateral expansion of the epitheca above the girdle, or, the sides of the lower half of the epitheca may be parallel, then enlarging very slightly; maximum epithecal width is reached two thirds of the epithecal length above the girdle and is half, sometimes up to two thirds of the epithecal length; there may be a slight concavity of the left profile in the region of the precingular plates, or at mid epithecal length, so that the epitheca appears to be slightly curved to the left; the apex is rounded to truncately rounded; a ring pore is apparently always lacking. (See Fig. 3,C.)
Dimensions: In specimen examined: In full ventral aspect, girdle diameter 57μ; length epitheca 162μ; maximum epithecal width 85μ; length left profile of hypotheca from base of horn to girdle 42μ; length left horn 57μ;. *From literature:* diameter 60–65μ (80μ according to Lemmermann); length epitheca 160–200μ; maximum epithecal width 85–100μ; length left horn 60–65μ (76μ according to Lemmermann).
Distribution: A fairly rare species occurring in warm waters of all the oceans and in the Mediterranean (Alboran Sea). Graham & Bronikowsky classify it as a rare, strictly tropical shade species. (See Table 1.)

Section **Digitata** Jörgensen (1911): 12.

Diagnosis: Differs from the other Sections in the slighter dorsiventral compression of the body, in the fact that the epitheca is dorsiventrally convex-concave or with longitudinal folds, and in the marked curvature of the left antapical horn which is spinulate.

Peters (1932), Steeman Nielsen (1934) and Graham and Bronikowsky (1944) placed the species of this Section in the Subgenus *Biceratium*. Jörgensen (1920) wrote: "As I now have found that *C. digitatum* possesses the same two broad ventral and dorsal apical and the very same characteristic boat-shaped lateral plates as *C. gravidum*, I propose to extend the subgenus Poroceratium to comprise *C. digitatum* (and *C. Schröderi*)." This is not a categorical statement that the epithecal plates of *C. schroeteri* are as in other members of this Subgenus and there are no further references to the matter in the literature. With this reserve, *C. schroeteri* is retained in Section *Digitata*.

Ceratium digitatum subsp. **digitatum** Schütt (1895) Pl. 12, fig. 42, 1–6.

Pavillard (1907): 230; (1916): 13; Jörgensen (1911): 12, pl. 2, fig. 13; (1920): 6, fig. 1; Forti (1921): 32, pl. 1, fig. 14; Böhm (1931a): 350; Peters (1932): 28;

TABLE 1. Showing distribution and relative frequency, expressed as a percentage, of species of the Subgenus *Poroceratium* in samples from the line of NGY stations off Port Elizabeth. Apart from the * stations, net hauls examined from 100–0m. (Temperatures in °C.)

	MARCH							MAY						
NGY Stations.	**11***	**12**	**13**	**14**	**15**	**16**		**41***	**42**	**43**	**44**	**45**	**46**	*Spot records from other stations.*
Surface temperature	20·66	24·28	25·49	23·78	22·19	21·62		17·49	23·27	24·15	23·50	21·25	20·90	
Temperature at 100m	13·26 (at 50m)	17·53	19·65	19·52	18·73	18·61		16·66 (at 50m)	12·21	19·99	20·54	20·50	20·37	
No. slides examined	4	4	4	4	4	8		4	5	7	4	4	5	
Total number ceratia	601	191	233	267	270	241	1803	318	92	197	184	241	365	1397
C. GRAVIDUM	—	0·52%	0·43%	—	—	—	0·11%	—	—	—	—	1·24%	0·27%	0·29%
C. CEPHALOTUM	—	—	0·86%	—	—	—	0·11%	—	1·09%	—	—	0·41%	—	0·14%
C. PRAELONGUM	—	—	—	—	—	—	0·00%	—	—	—	—	—	—	0·00% NGY 30
C. DIGITATUM SSP. DIGITATUM	—	—	—	—	—	—	0·00%	—	—	—	—	—	—	0·00% NGY 76
C. DIGITATUM SSP. ROTUNDATUM	—	—	—	—	—	—	0·00%	—	—	—	—	0·41%	—	0·07%
C. SCHROETERI	—	—	—	—	—	—	0·00%	—	—	—	—	—	—	0·00% NGY 30

Steemann Nielsen (1934): 8, fig. 5; (1939): 6; Schiller (1937): 358, fig. 392; Schubert (1937): 383; Rampi (1939): 302, fig. 3; Graham & Bronikowsky (1944): 16, figs. 5, C–E; Gaarder (1954): 11; Taylor* (1966): 463;? Wood (1963b): 39, fig. 144.

"Typenkreise der Gattung Ceratium" Schütt (1892): 269, fig. 79, 11.
?"*C. digitatum var.*" Peters (1932): 28, pl. 4, fig. 19.

Description: The body is slightly dorsiventrally compressed in the region of the girdle, ventrally concave, dorsally convex; in the *epitheca*, the dorsiventral convex-concave curvature becomes more marked; about one third of the epithecal length above the girdle, the epitheca curves dorsally and slightly to the left at an angle of about 45° to almost 90°; the apical third is flatter, slightly more compressed, with the sides, until now almost parallel, tapering to a bluntly acuminate cuspidate apex, set somewhat to the left, in the blunt point of which is the apical pore. The *antapical horns* are dissimilar, the right relatively short and straight, the left much stouter, directed posteriorly for a very short distance, then curved dorsally to slightly dorsolaterally, through an angle of about 135°, so that the tip, which is recurved, lies almost level with, to anterior to, the girdle; the left horn is spinulate, with the thecal wall on the inside of the curve thickened along the suture between the antapical plates. (See Fig. 2, A, C; Fig. 4, D).

Dimensions: In single damaged specimen found: Girdle diameter in full dorsal aspect, 42μ; length epitheca, approximately 120μ; length recurved part of left horn, 75μ. *From literature:* Jörgensen (1911), girdle diameter in full vextral aspect, 50μ or more, seen sideways, 40–45μ; length epitheca 90μ; length right horn, 25μ.

Distribution: Rare warm water taxon, recorded from all the oceans and the Mediterranean. Graham and Bronikowsky classify it as a rare, intolerant tropical shade species. (See Table 1.)

The single damaged specimen found in the present survey was seen only from the dorsal side. The antapical horns were similar to those of Schütt's iconotype, but the typical blunt acuminate point of the epithecal apex was not apparent, possibly due to the position of the specimen. The left side of the epithecal apex was not rounded but bluntly angled.

Peters found and illustrated a specimen "*C. digitatum var.*", "die einen noch breiteren Vorderkörper besizt, als die von Jörgensen beschreibene breite *f. rotundatum*". No other description is given. In the figure, the antapical horns resemble those of Schütt's iconotype, but the epithecal apex is rounded. This could be due to the angle at which the specimen was drawn. If however the apex was indeed rounded, then the specimen differs sufficiently from Schütt's iconotype to be considered as a separate taxon. (See Fig. 2, B.)

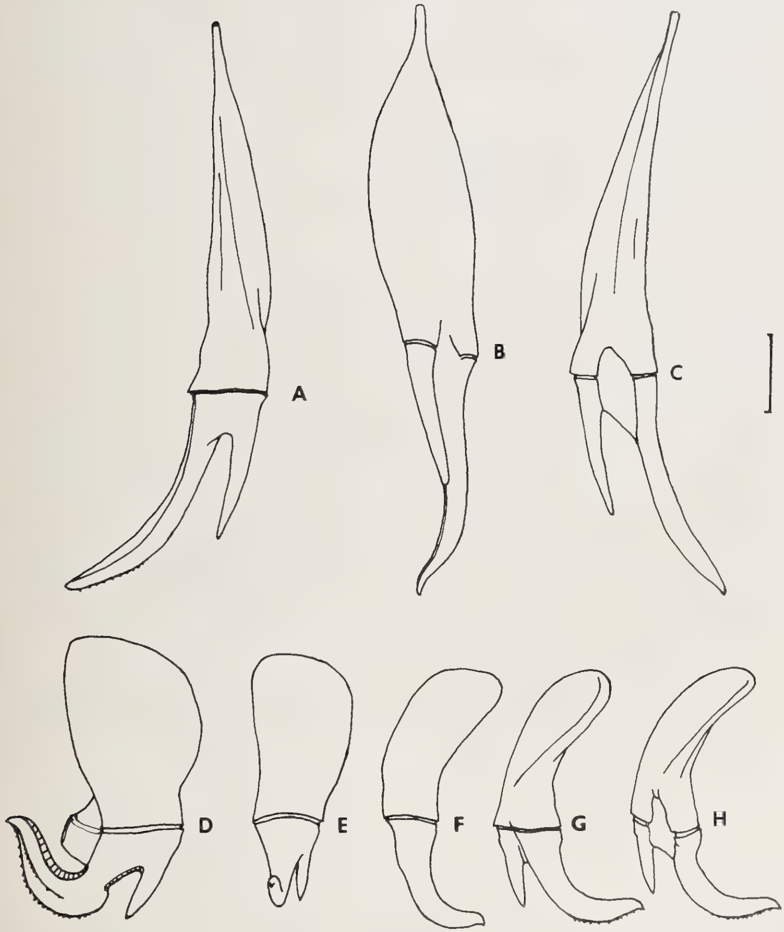

FIG. 4.

Fig. 4. *A*, *B* and *C*, *C. schroeteri: A*, dorsal aspect, thickening of thecal wall along outer side of left antapical horn shown in optical section; *B*, latero-ventral aspect; *C*, ventral aspect; *D*, broken specimen of *C. digitatum* subsp. *digitatum* ? dorsal view; *E*, *F*, *G* and *H*, *C. digitatum* subsp. *rotundatum* in dorsal, lateral, latero-ventral and ventral view. Camera lucida drawings of specimens from stations in the Agulhas current. (The scale line indicates 50μ.)

Graham & Bronikowsky noted little variation, except in the length of the left horn, in specimens of subsp. *digitatum* from the 26 stations at which it was found in the Carnegie samples.

Wood's inclusion of a ring pore in the upper third of the epitheca in a figure of subsp. *digitatum* is questioned. There is no mention in the literature of a ring pore in the species.

Ceratium digitatum subsp. **rotundatum** (Jörgensen) Reinecke stat. nov.

C. digitatum var. rotundatum Jörgensen (1920): 7, fig. 2a, b; Böhm (1931a): 350; Graham & Bronikowsky (1944): 16, fig. 5, A, B; Gaarder (1954): 11, fig. 12.

Diagnosis: Differs from the type in the less marked dorsal curvature of the left antapical horn, the tip of which lies some distance posterior to the girdle, and in the rounded apex of the epitheca.

Description: The *epitheca* is compressed, dorsiventrally convex-concave and curved as in the type, except that the curvature is more lateral; the epithecal apex is rounded, with the apical pore laterally placed. The *left antapical horn* which is spinulate, with the wall thickened as in the type, curves gradually laterodorsally, at an angle not exceeding 90° so that the tip, which is recurved, lies some distance posterior to the girdle. (See Fig. 4, E–H.)

Dimensions: In specimen examined: Semi-lateral girdle diameter, 42μ; approximate length epitheca, 120μ; distance from left side of girdle to tip of left horn, 96μ. *From literature:* Jörgensen (1920), girdle diameter, 59μ; Gaarder (1954), diameter 42μ; length 175μ.

Distribution: Extremely rare. Recorded from the Mediterranean (Jörgensen 1920, Böhm 1931a), South of the Azores (Gaarder 1954), in the Guinea Current (Jörgensen 1920), South of Easter Island (Graham & Bronikowsky 1944) and in the Agulhas Current. (See Table 1.)

The differences between this taxon and the type are sufficiently great to justify a taxonomic status exceeding that of variety. Examination of more specimens may warrant its treatment as a separate species. Graham and Bronikowsky found no intergrades between subsp. *digitatum* and the two specimens of subsp. *rotundatum* found in the Carnegie samples.

Ceratium schroeteri Schröder (1906): 368, fig. 43.

Kofoid (1907): 173, pl. 3, figs. 18, 19; Jörgensen (1911): 12, pl. 2, fig. 14; (1920): 8, fig. 3; Böhm (1931a): 350; Pavillard (1931): 67, pl. 2, fig. 15; Schiller (1937): 358, fig. 391; Silva (1956): 67, pl. 12, figs. 1–3; Wood (1963b): 42, fig. 150; Taylor* (1966): 463.

Description: The body is slightly dorsiventrally compressed in the region of the girdle; the *epitheca* in full ventral aspect is narrowly conical, tapering gradually towards the tip, very slightly inclined laterally to the left; on the right, the epitheca is expanded dorsolaterally into a longitudinal fold or hollow keel visible from the front, which rises a short distance above the girdle; a similar fold, not as sharply defined, arises on the ventral side above the ventral area; both expand gradually, then narrow a short distance behind the epithecal tip giving the epitheca in semilateral aspect a lanceolate profile with a short ill-defined apical horn; a third poorly defined fold is found on the dorsal side. The *antapical horns* are dissimilar, the right about half the length of the left straight or slightly curved to the left; the left horn is spinulate, dorsolaterally curved in a gradual arc; the tip may be recurved; the thecal wall of the left horn is thickened at the suture between the antapical plates along the inside of the curve. (Schroder illustrates a similar thickening along the edge of the right fold of the epitheca, not seen in the Agulhas specimen.) See Fig. 4 A–C.)
Dimensions: In single specimen found: Semi-lateral diameter, 42μ; length epitheca, 222μ; distance from tip of left horn to girdle, 130μ; the same for the right horn, 72μ; *From literature:* Total length, 335–342μ; diameter, 47–50μ; length epitheca, 203–212μ.
Distribution: Extremely rare warm water species recorded from all the oceans and the Mediterranean. (See Table 1.)

Section **Lanceolata** Jörgensen (1911): 13.

Diagnosis: Differs from the other Sections in the dorsiventral compression of the body together with the lanceolate shape of the epitheca, as seen in full ventral aspect, and in the nature of the epithecal apex which is a truncated point.

Ceratium lanceolatum Kofoid (1907): 172, pl. 3, fig. 17.

Jörgensen (1911): 13, pl. 2, fig. 15; Schiller (1937): 358, fig. 390; Gaarder (1954): 13, fig. 13.

?"Typenkreise der Gattung Ceratium" Schutt (1892): 269, fig. 79, 10b.

Description: The *epitheca* is dorsiventrally very compressed above the ventral area; in full ventral aspect it is lanceolate, with the apex a truncated point. The antapical horns are directed posteriorly, the right about the half length of the left. Ring pore apparently absent. (See Fig. 2 E.)
Dimensions: From the literature: Kofoid (1907), diameter, 19–22μ; length 95–122μ; Gaarder (1954), diameter, 56μ; length 285μ.
Distribution: Apparently only recorded twice, West of Peru (Kofoid 1907) and West of the Azores (Gaarder 1954), (and possibly the record of Schütt 1892).

The figure given by Schütt illustrates a specimen approximating the dimensions given by Gaarder. A teardrop shaped structure is shown in the middle of the epitheca, which, when compared with the illustration of the ring pore in the adjacent figure of *C. cephalotum*, appears to represent a ring pore.

Distribution of the Subgenus Poroceratium in the Area studied.

During International Geophysical Year 1958, 76 N50V net samples were taken at 100–0m and 50–0m, from stations in the Agulhas current along offshore lines between Durban and Plettenberg Bay, during three cruises in February and March, May and August of 1958.

An assessment of the relative frequency of the diatoms and armoured dinoflagellates was made by examining diluted drops of the samples and recording the first 300 to 600 diatom cells, (depending upon density), and the armoured dinoflagellates encountered during the process. A total of 30,323 diatom cells and 974 armoured dinoflagellates, of which 417 were ceratia, was counted. The numbers of armoured dinoflagellates recorded in this way ranged from 0 per 600 diatom cells to 125 per 310 diatoms. The percentages of ceratia relative to the total number of diatoms and armoured dinoflagellates, and to the number of dinoflagellates alone, were 1·33% and 42·61% respectively.

Samples collected during the March and May cruises from a line of 6 stations off Port Elizabeth, were examined in more detail for their ceratium flora.

The relative rarity of the species of the Subgenus *Poroceratium* in this area is indicated by their absence from the general diatom-armoured dinoflagellate count, and their low percentage frequency in the detailed examination of the Port Elizabeth line samples. (See Table 1.)

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A PRELIMINARY CHECK-LIST TO THE PTERIDOPHYTA AND SPERMATOPHYTA OF THE GRASSLAND AND SWAMP COMMUNITIES OF THE NGOYE FOREST RESERVE, ZULULAND

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Abstract

A check-list to the plant species of the grassland and swamp communi es in the Ngoye Forest Reserve is presented. A brief floristic analysis is included.

Uittreksel

'N VOORLOPIGE KONTROLELYS VAN DIE PHERIDOFIETE EN SPERMATOFIETE VAN DIE GRASVELD EN MOERASGEMEENSKAPPE IN DIE NGOYE WOUDRESERVAAT, ZULULAND.

'n Kontrolelys van die plantsoorte van die grasveld en moerasgemeenskappe in die Ngoye Woudreservaat word aangebied. 'n Beknopte floristiese ontleding word ingesluit.

Introduction

The Ngoye Forest Reserve is situated on the summit of the Ngoye Mountain in the Mtunzini District of Zululand at an altitude between 200 and 450 m above sea-level. Floristically the vegetation belongs to the humid coastal subtropical type.

The largest portion of the reserve is covered by forest, whilst the remainder consists of grassland and swamp communities. The latter communities are relatively small and are found along streams, in depressions and on hill-slope seepages.

Although the forest and its surrounds have been known to botanists for nearly a century and although the object of many a dispute on its protection, relatively little collecting and botanical work was undertaken in the past. This list was thus compiled as a preliminary index to the species of the grassland and swamps. A more comprehensive, annotated check-list including the forest species is envisaged for the future.

An analysis of the check-list shows that the Gramineae, 54 species; Compositae, 44 species; Leguminosae, 30 species; Cyperaceae, 19 species; and Liliaceae, 18 species; are the families best represented. The largest genera are *Helichrysum*, 12 species; *Senecio*, 11 species; *Eragrostis*, 5 species; *Hyparrhenia*, *Hypoxis*, *Indigofera*, *Lasiosiphon*, *Panicum*, *Scilla*, and *Scleria*, 4 species.

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The check-list is compiled from herbarium specimens of species collected and species observed during various visits of the author to the reserve.

Genera of the Pteridophyta have been arranged according to Schelpe (1969). The genera of the Spermatophyta have been arranged after Dalla Torre et Harms (Phillips, 1951). Species have been listed alphabetically.

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Schelpe, E. A. C. L. E., 1969. Revised Check-list of the Pteridophyta of Southern Africa. *Jl S. Afr. Bot.* **35**: 127–140.

Pteridophyta

Lycopodiaceae

Lycopodium carolinianum L.
L. cernuum L.

Selaginellaceae

Selaginella dregei (Presl) Hieron.

Schizaeaceae

Mohria caffrorum (L.) Desv.

Dennstaedtiaceae

Pteridium aquilinum (L.) Kuhn

Adiantaceae

Pteris vittata L.
Cheilanthes multifida Sw.
Pellaea quadripinnata (Forsk.) Prantl
P. viridis (Forsk.) Prantl var. glauca Sim

Thelypteridaceae

Thelypteris dentata (Forsk.) E. St. John

Gymnospermae

Stangeriaceae

Stangeria eriopus (Kuntze) Nash

Cycadaceae

Encephalartos ngoyanus Verdoorn

Angiospermae

Gramineae

Imperata cylindrica (L.) Beauv.
Eriochrysis pallida Munro
Eulalia villosa (Thunb.) Nees
Ischaemum arcuatum (Nees) Stapf
Hemarthria altissima Stapf & C. E. Hubb.
Coelorhachis capensis Stapf
Trachypogon spicatus (L.f.) Kuntze
Elyonurus argenteus Nees
Andropogon shirensis Hochst.
Schizachyrium semibere Nees
Cymbopogon validus Stapf & Burtt Davy
Hyparrhenia cymbaria (L.) Stapf
H. dissoluta (Nees) C. E. Hubb.
Hyparrhenia cf. H. dregea Stapf
H. filipendula (Hochst.) Stapf
H. gazensis (Rendle) Stapf
H. hirta (L.) Stapf
Monocymbium ceresiiforme (Nees) Stapf
Sorghastrum rigidifolium (Stapf) L. Chippindall
Themeda triandra Forsk. var. imberbis (Retz.) A. Camus
Paspalum commersonii Lam.
P. dilitatum Poir.
P. distichum L.
Panicum dregeanum Nees
P. hymeniochilum Nees var. glandulosum Nees
P. maximum Jacq.
P. natalense Hochst.

Gramineae—*Continued*

Alloteropsis semialata (R. Br.) Hitchc.
Brachiaria brizantha (Hochst.) Stapf
B. humidicola (Rendle) Schweick.
Sacciolepis curvata (L.) Chase
Digitaria argyrograpta (Nees) Stapf
D. macroglossa Henr.
Rhynchelytrum repens (Willd.) C. E. Hubb.
Setaria rigida Stapf
S. sphacelata (Schumach.) Stapf & C. E. Hubb ex M. B. Moss
Stenotaphrum secundatum (Walt.) Kuntze
Leersia hexandra Sw.
Ehrharta erecta Lam. var. natalensis Stapf
Aristida junciformis Trin. & Rupr.
Sporobolus africanus (Poir.) Robyns et Tournay
S. centrifugus Nees
S. pyramidalis Beauv.
Tristachya hispida (L.f.) K. Schum.
Trichopteryx dregeana Nees
Cynodon dactylon (L.) Pers.
Ctenium concinnum Nees
Dactyloctenium australe Steud.
Eragrostis atrovirens (Desf.) Trin.
E. capensis (Thunb.) Trin.
E. curvula (Schrad.) Nees
E. racemosa (Thunb.) Steud.
E. superba Peyr.
Stiburus alopecuroides (Hack.) Stapf

Cyperaceae

Ascolepis capensis Ridley
Cyperus isocladus Kunth
C. obtusiflorus Vahl
Pycreus ferrugineus C.B. Cl.
P. polystachyos Beauv.
Kyllinga cf. K. elatior Kunth
Fuirena chlorocarpa Ridley
Fimbristylis dichotoma (L.) Vahl
F. hygrophila Gordon-Gray
F. monostachyos Hassk.
Bulbostylis contecta (Nees) Gordon-Gray
Rhynchospora corymbosa (L.) Britt.
R. glauca Vahl
R. mauritii Steud.
Schoenoxiphium cf. S. caricoides C.B. Cl.
Scleria melanomphala Kunth
S. natalensis C.B. Cl.
S. nutans Willd. ex Kunth
S. species (H. J. T. Venter 2380)—undescribed

Araceae

Stylochiton natalense Schott

Xyridaceae

Xyris anceps Lam.
X. capensis Thunb.

Eriocaulaceae

Eriocaulon sonderianum Koern.

Commelinaceae

Commelina africana L.
C. benghalensis L.
C. eckloniana Kunth
Cyanotis speciosa (L.f.) Hassk.

Juncaceae

Juncus lomatophyllus Spreng.

Liliaceae

Androcymbium longipes Bak.
Bulbine frutescens (L.) Willd.
Anthericum angulicaule Bak.
A. saundersiae Bak.
Chlorophytum krookianum Zahlbr.
Kniphofia laxiflora Kunth
Aloe umfoloziensis Reynolds
A. arborescens Mill.
Agapanthus campanulatus Leight. subsp. patens Leight.
Albuca setosa Jacq.
A. species (H. J. T. Venter 2492)
Scilla cooperi Hook.f.
S. natalensis Planch.
Scilla cf. S. polyantha Bak.
Scilla cf. S. sandersonii Bak.
Resnova schlechteri (Bak.) v. d. Merwe
Eucomis cf. E. pole-evansii N. E. Br.
Ornithogalum virens Lindl.
Asparagus africanus Lam.

Amaryllidaceae

Anoiganthus breviflorus (Harv.) Bak.
Cyrtanthus contractus N.E. Br.
Hypoxis argentea Harv.
H. filiformis Bak.
H. membranacea Bak.
H. rooperi S. Moore

Dioscoreaceae

Dioscorea sylvatica Eckl.

Iridaceae

Aristea cognata N. E. Br.
A. woodii N.E. Br.
Dierama elatum N.E. Br.
Tritonia cf. T. lineata Ker
Gladiolus crassifolius Bak.
Gladiolus cf. G. papilio Hook.f.
Lapeirousia laxa (Thunb.) N.E. Br.
Watsonia densiflora Bak.

Orchidaceae

Habenaria woodii Schltr.
Satyrium longicauda Lindl.
Schizochilus zeyheri Sond.

Orchidaceae—*Continued*

Disa caffra Bol.
D. polygonoides Lindl.
Polystachya pubescens Reichb.f.
Eulophia speciosa (R. Br. ex Lindl.) Bol.
E. parviflora (Lindl.) Hall

Proteaceae

Protea multibracteata Phill.

Santalaceae

Thesium costatum A. W. Hill
T. natalense Sond.

Polygonaceae

Polygonum pulchrum Blume

Phytolaccaceae

Psammotropha myriantha Sond.

Cruciferae

Heliophila elongata (Thunb.) DC.

Droseraceae

Drosera burkeana Planch.
D. madagascariensis DC.

Crassulaceae

Cotyledon zuluensis Schonl.
Kalanchoe rotundifolia Haw.
Crassula ericoides Haw.
C. heterotricha Schinz
C. rubicunda E. Mey.

Rosaceae

Cliffortia serpyllifolia Cham. & Schlechtd.

Leguminosae

Cassia biensis (Stayaert) Mendoca & Torre
C. mimosoides L.
Aspalathus gerrardii Bol.
Dichilus strictus E. Mey.
Crotalaria natalensis Bak.f.
Argyrolobium harveianum Oliv.
A. rupestre (Eckl. & Zeyh.) Walp.
A. tuberosum Eckl. & Zeyh.
A. species (H. J. T. Venter 2365)
Indigofera cylindrica DC.
I. hedyantha Eckl. & Zeyh.
I. sanguinea N.E. Br.
I. tristis E. Mey.
Psoralea pinnata L.
Tephrosia grandiflora (Ait.) Pers.
T. longipes Meisn.
T. macropoda (E. Mey.) Harv.
T. polystachya E. Mey.
Zornia capensis Pers.
Desmodium canum (J. F. Gmel.) Schinz & Thell.
D. dregeanum Benth.
D. hirtum Guill. & Perr.
Pseudarthria hookeri Wight & Arn.
Dalbergia obovata E. Mey.
Rhynchosia stenodon Bak.f.
R. totta (Thunb.) DC.
Eriosema cordatum E. Mey.
E. parviflorum E. Mey.
E. salignum E. Mey.
Vigna vexillata (L.) Benth.

Geraniaceae

Pelargonium alchemilloides (L.) Ait.
P. luridum (Andr.) Sweet

Oxalidaceae

Oxalis semiloba Sond.

Linaceae

Linum thunbergii Eckl. & Zeyh.

Polygalaceae

Polygala capillaris E. Mey.
P. rehmannii Chod.
P. hottentotta Presl.

Euphorbiaceae

Phyllanthus meyerianum Muell. Arg.
Adenocline bupleuroides Prain
Acalypha peduncularis E. Mey.
Clutia abyssinica Jaub. & Spach. var. abyssinica
C. pulchella L.

Callitrichaceae

Callitriche bolusii Schonl. & Pax ex Marl.

Anacardiaceae

Rhus discolor E. Mey.

Celastraceae

Maytenus nemorosa (Eckl. & Zeyh.) Marais

Hippocrateaceae

Salacia kraussii (Harv.) Harv.

Vitaceae

Rhoicissus tridentata (L.f.) Wild & Drumm.

Tiliaceae

Triumfetta pilosa Roth. var. effusa (E. Mey. ex Harv.) Wild

Malvaceae

Sida cordifolia L.
Hibiscus diversifolius Jacq. subsp. diversifolius

Guttiferae

Hypericum aethiopicum subsp. sonderi (Bred.) Robs.
H. lalandii Choisy

Thymelaeaceae

Lasiosiphon anthylloides Meisn.
L. caffer Meisn.
L. kraussii Meisn.
L. splendens Endl.
Arthrosolen calocephalus (Meisn.) C. A. Mey.
Passerina filiformis L.

Myrtaceae

Eugenia albanensis Sond.

Melastomataceae

Dissotis canescens (Grah.) Hook.f.

Halorrhagidaceae

Laurembergia repens Berg.

Umbelliferae

Centella coriacea Nannfd.
C. glabrata L. var. natalensis Adams.
Alepidea gracilis Bumm. var. major Weim.

Primulaceae

Lysimachia ruhmeriana Vatke

Ebenaceae

Diospyros galpinii (Hiern) De Wint.
D. whyteana (Hiern) F. White

Gentianaceae

Sebaea sedoides Gilg.
Belmontia grandis (E. Mey.) Steud.

Asclepiadaceae

Xysmalobium involucratum (E. Mey.) Decne.
X. undulatum (L.) Ait.F.
Pachycarpus concolor E. Mey.
Asclepias burchellii Schltr.
Brachystelma flavidum Schltr.

Convolvulaceae

Convolvulus farinosa L.
Ipomoea obscura (L.) Ker-Gawl. var. fragilis (Choisy) A. Meeuse
I. obscura (L.) Ker-Gawl. var. obscura

Labiatae

Leonotis dysophylla Benth.
Stachys nigricans Benth.
Pycnostachys reticulata (E. Mey.) Benth.
Plectranthus calycinus Benth.
P. tomentosus Benth.
Syncolostemon argenteus N.E. Br.
S. densiflorus E. Mey.
Thorncroftia thorncroftii (S. Moore) Codd

Solanaceae

Solanum incanum L.

Scrophulariaceae

Zaluzianskya maritima Walp.
Selago hyssopifolia E. Mey.
Alectra orobanchoides Benth.
A. sessiliflora (Vahl) Kuntze
Sopubia simplex Hochst.
Buchnera glabrata Benth.
Cycnium adonense E. Mey.
Striga bilabiata (Thunb.) Kuntze

Lentibulariaceae

Utricularia prehensilis E. Mey.

Acanthaceae

Thunbergia atriplicifolia E. Mey. ex Nees
Chaetacanthus setiger (Pers.) Lindl.
Asystasia gangetica (L.) T. Anders.
Decliptera zeylanica Nees
Justicia protracta (Nees) T. Anders.

Rubiaceae

Kohautia amatymbica Eckl. & Zeyh.
Oldenlandia cephalotes (Hochst.) Kuntze
O. herbacea (L.) Roxb.
Pentas angustifolia (A. Rich. ex DC.) Verdc.
Pentanisia prunelloides (Kl. ex Eckl. & Zeyh.) Walp.
Pachystigma latifolium Sond.
Anthospermum herbaceum L.f.
Richardia brasiliensis (Moq.) Gomez
Diodia natalensis (Hochst.) Garc.

Dipsacaceae

Cephalaria pungens Szabó
Scabiosa columbaria L.

Cucurbitaceae

Cucumis zeyheri Sond.

Campanulaceae

Cyphia elata Harv.
Lobelia alata Labill.
Monopsis belliflora E. Wimm.
M. scabra (Thunb.) Urb.

Compositae

Vernonia corymbosa Less.
V. hirsuta Sch. Bip.

Compositae—*Continued*

V. kraussii Sch. Bip.
Aster muricatus Less.
Nidorella auriculata DC.
Laggera alata (D. Don.) Sch. Bip. ex Oliv.
Helichrysum adenocarpum DC.
H. adscendens Less.
H. appendiculatum Less.
H. aureo-nitens Sch. Bip.
H. decorum DC.
H. foetidum (L.) Cass.
H. kraussii Sch. Bip.
H. longifolium DC.
H. miconiaefolium DC.
H. nudifolium (L.) Less. var. nudifolium
H. nudifolium (L.) Less. var. quinquenerve (Thunb.) Moeser
H. panduratum O. Hoffm.
H. stenopterum DC.
Athrixia phyllicoides DC.
Aspilia mossambicensis (Oliv.) Wild
A. natalensis (Sond.) Wild
Athanasia punctata (DC.) Harv.
Schistostephium crataegifolium Fenzl
Cineraria deltoidea Sond.
Senecio bupleuroides DC.
S. erubescens Ait. var. incisus DC.
S. fibrosus O. Hoffm.
S. inophyllus Phill. & C.A. Sm.
S. latifolius DC.
S. oxyodontus DC.
S. oxyriaefolius DC.
S. pterophorus DC.
S. ruderalis Harv.
S. serratuloides DC.
S. speciosus Willd.
Gamolepis debilis Harv.
Osteospermum grandidentatum DC.
Gazania krebsiana Less. subsp. serrulata (DC.) Roessl.
Berkheya radula (Harv.) De Wild.
B. setifera DC.
Gerbera natalensis Sch. Bip.
G. piloselloides Cass.
Hypochoeris radiata L.
Lactuca capensis Thunb.
Crepis hypochaeridea DC.

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ANATOMICAL ASPECTS OF GROWTH PROLIFERATION IN *NICOTIANA TABACUM* TISSUE CULTURED *IN VITRO*[1]

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Abstract

Aspects of the anatomy of tobacco stem explants and subcultured callus, growing on a nutrient medium to which varying ratios of auxin and cytokinin were added, were studied. Callus formed during explant growth generally originated from the xylem ray parenchyma, either centrifugal or centripetal to the parent xylem. Internal phloem bundles, as well as phloem parenchyma and cambial derivatives, if present, also gave rise to new growth. The pith rarely produced callus. Roots, diarch, triarch or polyarch, often di- or polystelic, produced root hairs which grew in between callus cells. Buds developed large, multicellular trichomes at the bases of which stomata with photosynthetic guard cells were frequently observed. High auxin appeared to stimulate tracheid formation and high cytokinin the density of the developing xylem.

Uittreksel

ANATOMIESE ASPEKTE VAN DIE GROEIVERMEERDERING IN *NICOTIANA TABACUM* WEEFSEL *IN VITRO* GEKWEEK. Aspekte van die anatomie van tabak stingel-eksplante en gesubkultiveerde kallus wat op 'n voedingsmedium onder verskillende auksien en sitokinien regimes gekweek is, is bestudeer. Kallus wat op die eksplante ontwikkel blyk hoofsaaklik uit die vaatstrale van die xileem te ontspring, hoewel interne floëembondels, en floëemparenchiem en kambiale derivate, indien aanwesig, ook tot kallusproduksie aanleiding kon gee. Die murgparenchiem het slegs by uitsondering kallusweefsel geproduseer. Wortels, twee-, drie- en meerstralig, dikwels met twee of meer vaatstele, is opgemerk, met wortelhare wat tussen die kallusparenchiem deurgroei. Knoppe met groot, multisellulêre hare op die basisse waarvan huidmondjies met fotosintetiserende sluitselle dikwels voorgekom het, is algemeen opgemerk. Hoë auksientoedienings het die aantal trageiede gestimuleer terwyl hoë sitokinientoedienings die digtheid van die xileemmasse beïnvloed het.

Introduction

This study and those reported on in two subsequent papers were concerned primarily with the sequence of events by which certain morphological characteristics develop in tobacco callus in response to varying ratios of the plant growth hormones, auxin and cytokinin. The main objective was to gain a basic understanding of the anatomy of structural development in tobacco

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tissue cultured *in vitro*, in the hope that this would serve as a basis for further investigations—especially of histochemical, microautoradiographical and ultrastructural aspects—of growth and development of cultured tissues in general.

The present biochemical and physiological bias of plant tissue culture research has resulted in at least a partial neglect of basic anatomical and histogenic considerations; and, while it is generally conceded that tissue obtained by the *in vitro* subculturing of plant material is, because of its greater structural simplicity, easier to work with than the intact plant itself, this poses a fundamental problem. Karstens (1965) namely questions whether data obtained from the investigation of cultured tissues can be compared with phenomenological situations in the intact plant. Skoog (1957) maintains that plant growth and differentiation of all types is determined by quantitative levels and proportions of various growth factors, and that it would be meaningless to describe anatomical and morphological features of cultured tissues as if certain forms of growth are fixed without detailed reference to the precise conditions of growth. However, it is clear that the contributory factors to certain forms of growth can be viewed in perspective only if the basic anatomy of the original as well as the developing plant tissue is known.

In vitro culture of excised organs, tissues, and cells of higher plants has opened new approaches for studying plant cell and tissue physiology, particularly the biochemistry of morphogenesis and its control. Anatomical and physiological features of growth and development in cultured tissues are complementary and it would appear entirely fruitless to draw conclusions on the effect of, say, a particular growth substance on differentiation without relating this to, for example, the anatomical simplicity or complexity of the starting material.

For valid comparisons to be drawn between intact and cultured plants it is therefore essential that the basic structures and processes of cultured tissue be fully understood.

Material and methods

Explant Technique. Defoliated stems of succulent, vigorously growing *Nicotiana tabacum* (cv. Kutsaga 614) plants were sterilised by first plunging them into 70% ethanol. After thorough scrubbing, the stems were soaked in 0·35% sodium hypochlorite for 15 minutes, followed by three rinses with sterile distilled water. Four-centimetre segments were then cut and placed in sterile petri dishes. Prior to transferring to nutrient agar, one-half a centimetre of tissue was trimmed off either end and the remaining segment divided into three 1 cm pieces. The bark was then peeled away and the segments were either

FIGS. 1–4.

Tobacco callus and shoots growing on media containing different ratios of indoleacetic acid (IAA) and kinetin (CK), mg/l, respectively. Fig. 1. Loose and frosty to even and compact callus; 4·0:1·2. Fig. 2. Compact, irregularly lobed callus which did not give rise to roots but from which buds subsequently developed; 4·0:0·08. Fig. 3. Vegetative bud developing from explant on which little callus has formed; zero: 0·08. Fig. 4. Numerous buds and leafy shoots developing from explant following considerable callus formation; 4·0:0·08. Bar represents 1 cm.

b, bud; c, callus


ac
vb
b
pp
ex
x
ac
ug
5
gc

halved or quartered. Each tissue piece was finally plunged into 70% ethanol followed by a rinse in sterile distilled water before being seated on the agar. All excisions and transfers were carried out in sterile transfer rooms.

Culture Media and Conditions. Synthetic growth media were prepared following Vasil and Hildebrandt's (1966) modification of Murashige and Skoog's (1962) medium for tobacco tissue. Auxin solutions were made by dissolving the appropriate amount of indoleacetic acid (IAA) in a few drops of 70% ethanol before diluting to volume with glass-distilled water. Kinetin (6-furfurylaminopurine) solutions were prepared by first steaming in a small volume of distilled water for about 20 minutes in an autoclave. After cooling the solutions were made to volume with glass-distilled water.

Vitamin and hormone stock solutions were prepared fresh and IAA was always made up immediately prior to use. To prevent the possible photo-inactivation of IAA by light, all final nutrient media were kept in the dark before, and for a period of three days after, transfer of the tissue. Tobacco stem explants and callus cylinders for subculture, were grown on 50 ml nutrient agar in 250 ml wide-mouth erlenmeyer flasks or on 15 ml agar in test tubes under a 12-hour photoperiod of ca. 150 ft. candles at 23 ± 3°C. The pH of the media varied from 5·5 to 5·8.

Hormone Ratios. Six different treatments were used in which the ratio of auxin to cytokinin (CK) was varied as follows: IAA : CK mg/l (1) 4·0 : zero, (2) zero : 0·08, (3) 4·0 : 0·08, (4) 4·0 : 1·2, (5) zero : 5·0, and (6) 4·0 : 5·0.

Microtechnique. A considerable amount of work was based on fresh tissue sectioned either by hand or with a sliding microtome and stained with either toluidene blue, aniline blue or a polychrome dye. Permanent slides were prepared of callus fixed in 3% glutaraldehyde or 10% acrolein, dehydrated, infiltrated and embedded following Feder and O'Brien (1968). Stains used were safranin and Delafield's haematoxylin, and Fleming's triple stain (Johansen, 1940), and aniline blue (Jensen, 1962).

Gross Morphology of the Explant. The tobacco tissue from which the explants were taken was already undergoing secondary thickening. All tissues external to the xylem except probably some elements of the vascular cambium were removed when the bark was peeled off. The remaining explant consisted of a continuous band of xylem of regular, radial rows of vessels separated by

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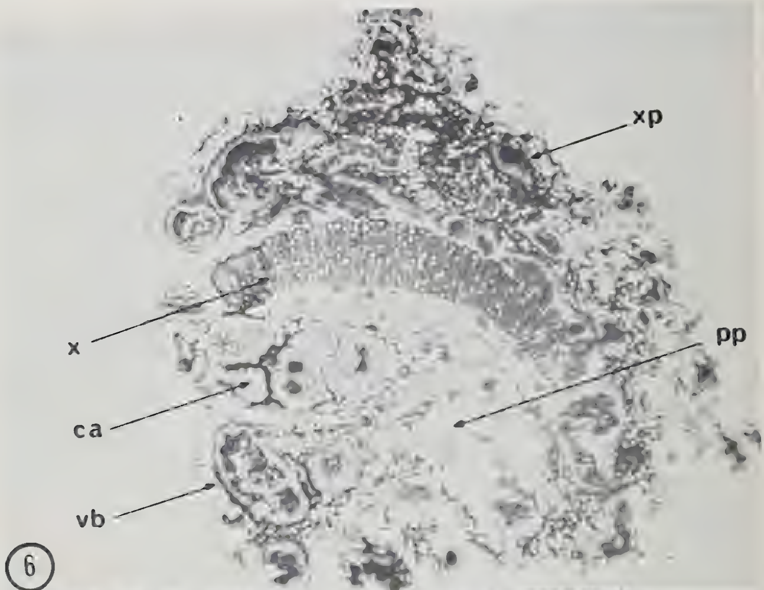
FIG. 5.

Transverse section of an explant showing callus developing from the external xylem surface as well as from peripheral internal phloem bundles. Note difference in texture between aerial callus and agar or underside callus. IAA:CK, 4·0:1·2 mg/l. Sliding microtome section of fresh tissue, polychrome stain. × 13.

ac, aerial callus; b, bud; ex, width of original explant; gc, giant cell; pp, pith parenchyma; ug, agar or underside callus, vb, vascular bundle; x, xylem.


xp
x
pp
ca
vb
6


x
vb
ca
7

rays of xylem parenchyma which, in older tissue, often possessed thickened walls. This band of xylem partially enclosed a pith consisting of storage parenchyma with regular, large intercellular spaces. Immediately centripetal to the xylem are groups of protoxylem elements as well as scattered bundles of internal phloem. These bundles have sieve tubes, companion cells, and phloem parenchyma as well as a lining of fibres on their inner sides. No continuous cambium is associated with the inner phloem.

Results and Discussion

Despite some inconsistencies, due perhaps to the heterogeneity of the initial plant material, the six different treatments in which auxin and cytokinin ratios were varied, most commonly elicited the following growth forms:

1. IAA : CK, 4·0 : zero mg/1. Callus development was rapid and chunky in appearance with a loose, frosty surface of large, extended cells overlying a light green zone of chloroplast-containing cells. Roots, often numerous and much branched, formed from original explants following vigorous callus growth.

2. Zero : 0·08 mg/1. As expected, negligible amounts of callus were produced; not infrequently vegetative buds would develop directly from explant surface.

3. 4·0 : 0·08 mg/1. A light-green, continuous callus formed on the external xylem surface. The callus was dense and frosty but by and large remained smooth; there was no pustular growth and normally numerous buds developed.

4. 4·0 : 1·2 mg/1. An even, compact layer of green-coloured callus covering the entire surface was produced. No shoots or roots were produced.

5. Zero : 5·0 mg/1. Negligible callus growth but numerous buds were observed in the tissues internal to the explant xylem.

6. 4·0 : 5·0 mg/1. Much callus developed, appearing crystalline, frosty and lumpy. This pale frosty callus of cells overlay a deep-green tissue.

Explants with a simple and uniform anatomical structure such as tissue pieces of pure parenchyma, are probably the most suitable for histogenic studies. Those with a complex anatomy are less suitable because cells of many different

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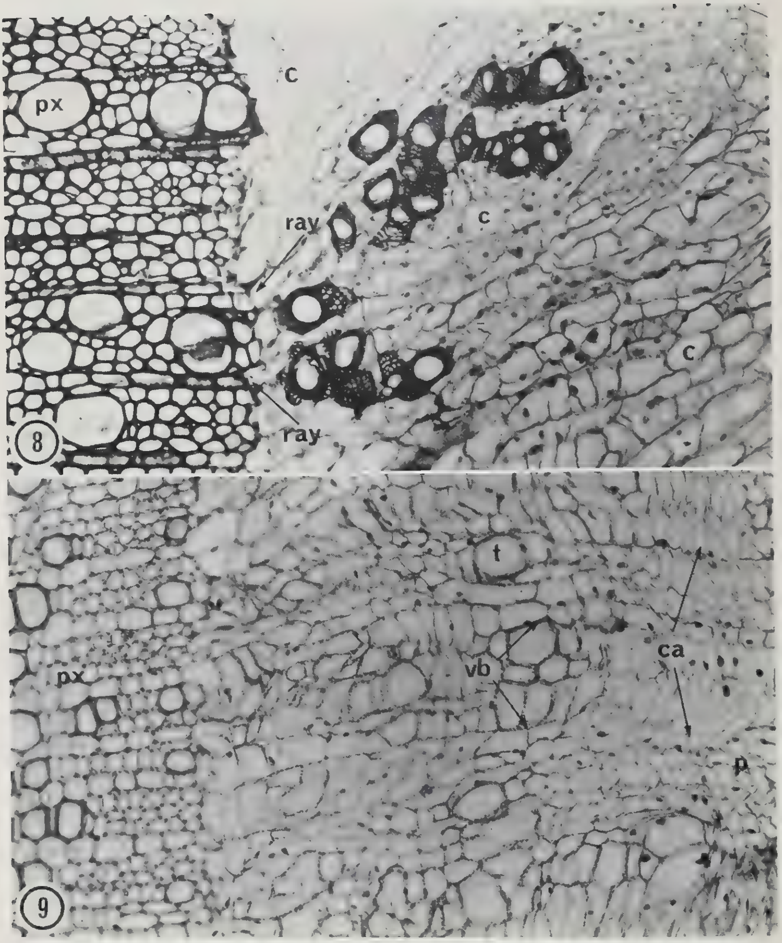
Figs. 6–7.

Sliding microtome sections of fresh material, polychrome stain. IAA:CK, 4·0:0·08 mg/1. Fig. 6. Transverse section of cultured stem segment showing xylem and rare instance of pith proliferation. Callus is compact, with numerous vascular bundles. × 12. Fig. 7. Higher magnification of Fig. 6. showing vascular bundles surrounded by cyclic cambial layers. × 25.
ca, cambial layers; pp, pith parenchyma; vb, vascular bundles;
x, xylem; xp, xylem proliferations.



FIGS. 8–9.

IAA:CK, 4·0:0·08 mg/l. ×160. Fig. 8. Transverse section of explant secondary xylem showing callus proliferation from xylem parenchyma of xylem ray, Fleming's triple stain. Fig. 9. In the proliferating callus a cambium with regular files of cells has formed and has produced tracheids and vascular nodules proximally and phloem distally, haematoxylin-safranin stain.

c, callus; ca. cambium; p, phloem; px, parent xylem; t, tracheid; vb, vascular bundle/nodule.

types, in various stages of differentiation and dedifferentiation, may contribute to callus proliferation, reducing the homogeneity of the subsequent tissue. The stem explants used in this study and in much of tobacco tissue culture research fall in the complex category and a great amount of variation, in fact, was encountered in the initial cultures. However, with subsequent subculturing growth forms became more uniform.

Figures 1–4 show some of the responses of tobacco stem explants to different ratios of auxin and cytokinin and Figs. 5–15 illustrate some of the interesting features to which further allusion is made below. Since in tobacco tissue culture the external phloem and most of the cambium presumably is removed during excision or destroyed in the sterilisation procedure, it is instructive to examine the origin of the callus produced in the subsequent cultures.

Origin of Callus

1. *Phloem parenchyma.* Phloem, if present, commonly gives rise to a thin layer of new growth as a result of a generalised proliferation of its parenchyma. In tobacco explants this type of growth is rare because, as previously pointed out, the phloem—and often also part of the cambium—is removed when the bark is peeled off in the explant technique. It was commonly observed, however, that the most superficial internal or intraxylary phloem bundles which were exposed by excision produced callus masses in which cambia frequently formed. (Fig. 5, ac, ng; Fig. 10, ca). Vegetative buds often formed immediately after pıoliferation of some callus from these phloem bundles, often without callus formation having occurred in other parts of the explant tissue. Rarely were the unexposed internal phloem bundles themselves observed to produce callus. The internal phloem imparts a measure of heterogeneity to the tobacco explant and while this type of tissue grows readily, interpretation of the results must take into consideration the controlling influences exerted by these centres of potential growth.

2. *Vascular cambium.* Commonly, the cambium, in those parts where it is undamaged, continues to divide and produces fine, downy flocks or pustules of new growth (Fig. 6, 7), the cells of which are large and intermingle to form a more or less continuous surface layer. Finally, the whole surface becomes greenish-white. Scattered vascular bundles of xylem and phloem appear, especially in treatments containing 4 mg/l IAA with little or no kinetin. Cambia regularly form at the boundary of parent tissue and are responsible for the development of the parenchymatous callus.

3. *Xylem parenchyma.* In the majority of cases the cambium of the explant is destroyed and a growth similar to that described above for cambial parenchyma originates from the cells of the xylem rays. Frequently, all the callus formed


ca
p
c
px
ip
pp
10

in explant growth originated from a single or a few xylem rays (Figs. 8–9). In localized regions parenchymal meristems develop, the cells of which seem to retain a higher proliferative capacity than do parenchyma cells in general. Their structure distinguishes them from the normal pith parenchyma: they are vacuolate with a thin parietal cytoplasm and small nuclei, but do not seem to elaborate starch or other storage products. Their degree of differentiation appears to be intermediate to that of common parenchyma and cells of the cambium, and this probably explains their tendency to divide.

4. *Pith parenchyma.* At a first glance it is strange that in most cases the pith itself does not proliferate. Jablonksi and Skoog (1954) failed to obtain cell division in excised tobacco pith even with high concentrations of IAA, such as 4 mg/l. It seems as though the parenchyma of the xylem rays requires less external stimulation to divide than those of the pith. Figures 6 and 7 also show one of the rare instances where the pith parenchyma in fact divided and produced a callus mass.

Cambial activity

With the proliferation of the xylem rays into a homogeneous parenchymal tissue, cambia become organised in one of two ways. They either form in more or less linear tangential rows giving rise to phloem centrifugally and xylem—in regular radial rows—centripetally (Figs. 9, 11, 12), or circular cambia develop producing isolated vascular nodules or islets (Fig. 7). Internal cambia are a result of the dedifferentiation and reorganisation of parenchymatous elements, but once formed they proliferate tissues as do regular cambia. Whether these secondarily formed cambia are diffuse or well-defined seems to depend on the density of the callus mass which, in turn, is influenced initially by the hormone concentrations applied and probably also by carbon sources, as well as other factors.

Invariably, a cambium-like meristem is formed immediately beneath the surface layers of the callus. The growth here is primarily an expansion growth. As a result of repeated divisions, tangential walls form in the superficial parenchyma followed later by cell walls which now appear to be laid down randomly, thus forming groups of cells the composing elements of which often

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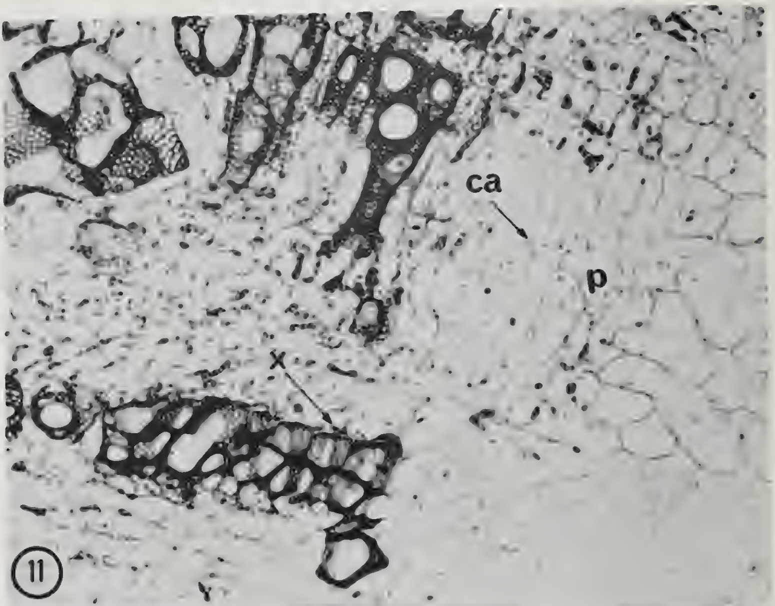
Fig. 10.

Transverse section of glutaraldehyde-fixed tissue piece, Fleming's triple stain. IAA:CK, 4·0:1·2 mg/l. Proliferation has occurred from the superficial intraxylary phloem bundles of the explant resulting in callus tissue in part of which a discrete cambium has formed regular, radial rows of cells. × 160.

c, callus; ca, cambium; ip, internal phloem; p, phloem; pp, pith parenchyma; px, parent xylem.


ca
p
x
11


cc
sm
12

exhibit radial arrangement. A layering results in which large lacunae are present in the outer zone.

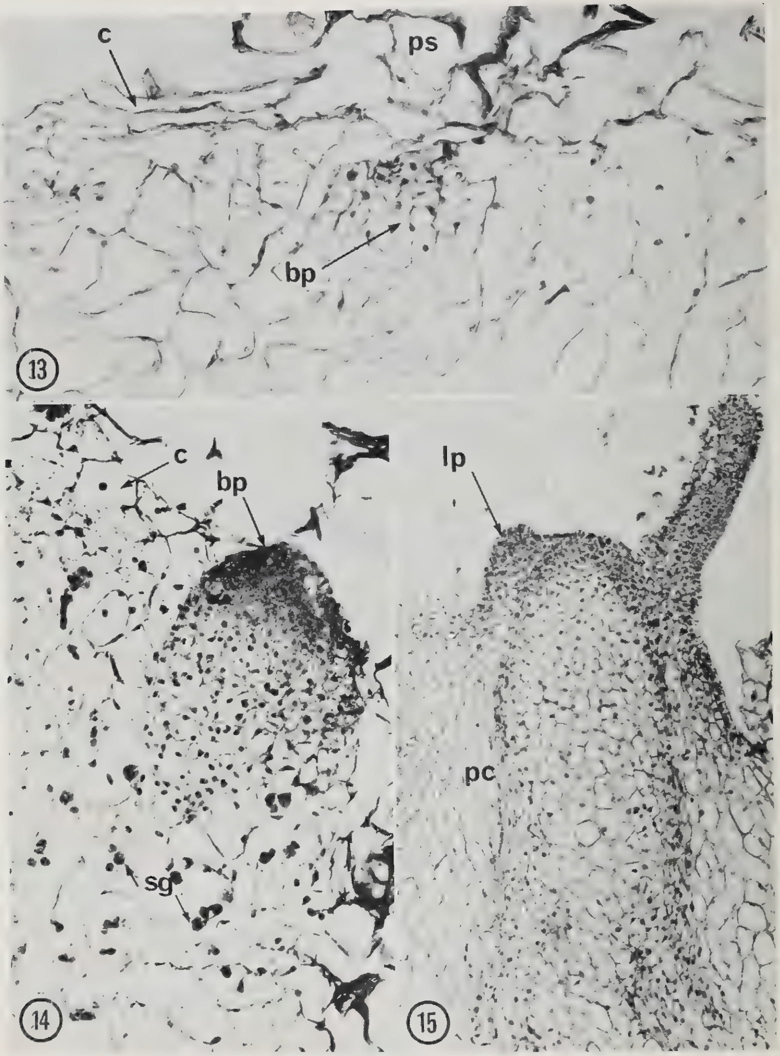
Spatial arrangement of new growth. Striking differences exist in structure between the new tissue growing into the nutrient medium and that developing into the air space above the agar. That into the agar consists of a fan-like proliferation forming a more compact, fairly regular meristematic tissue. The marginal cells of the proliferating tissue grow down into the agar and divide; the proximal division products are forced into close contact and form a compact tissue that remains actively dividing. There seem to be two ways in which this tissue keeps growing: (i) by pioneer action of the marginal cells; and (ii) by expansion caused by division of the cells of the adjoining tissue behind them. This explains the common observation of callus penetrating the agar surface, ultimately splitting it. Differentiation of cells, into tracheids for example, is exceedingly rare in this zone.

Above the agar, primary and secondary phases of growth may be recognised. The first phase corresponds to that in the agar except that the marginal cell columns are long and stretch out into the air space. The division products form a loose, irregularly constructed tissue of branches, often touching to form internal air spaces. Gautheret (1957) calls these more or less branched chains of cells "pseudothalli" and they are probably analogous to the "Wundhaare" of Magnus (1918). They remain free and do not intergrow. Through random divisions, however, they may lose their identity as all the air spaces (lacunae) become filled with cells. A full description of these pesudothalli is reported on in a subsequent paper. The secondary phase is that of differentiation and appears to depend on the concentration of IAA. Tracheids with scalariform or reticulate thickening and with walls which become lignified form in the pseudothalli.

Subcultured callus. The most common type of proliferation of subcultured callus is from the fundamental parenchyma. However, even such explants invariably contain vascular elements and vegetative growing points, the latter continuing development if the hormonal balance is conducive to either root or shoot formation or both. Growth is generally more uniform than is the case in stem explants, although vascular elements as well as vegetative meristems are formed in the same way.

FIGS. 11–12.

Histogenic differentiation in subcultured callus, Fleming's triple stain. IAA:CK, 4·0:1·2 mg/1. Fig. 11. Well-delineated cambium producing perforated tracheary elements and phloem. ×150. Fig. 12. Higher magnification of Fig. 10, showing detail of phloem. ×400. ca, cambium; cc, companion cell; p, phloem; sm, sieve tube member; x, xylem.



FIGS. 13–15.

Glutaraldehyde-fixed sections, haematoxylin-safranin stain. IAA:CK, 4·0:1·2 mg/l. × 160. Fig. 13. Very young stage of bud initiation indicated by group of meristematic cells constituting a bud primordium. Fig. 14. Developing bud primordium. Fig. 15. Longisection of a young bud with leaf primordium.

c, callus; bp, bud primordium; lp, leaf primordium; pc, procambial strand; ps, pseudothallial zone; sg, amyloplasts.

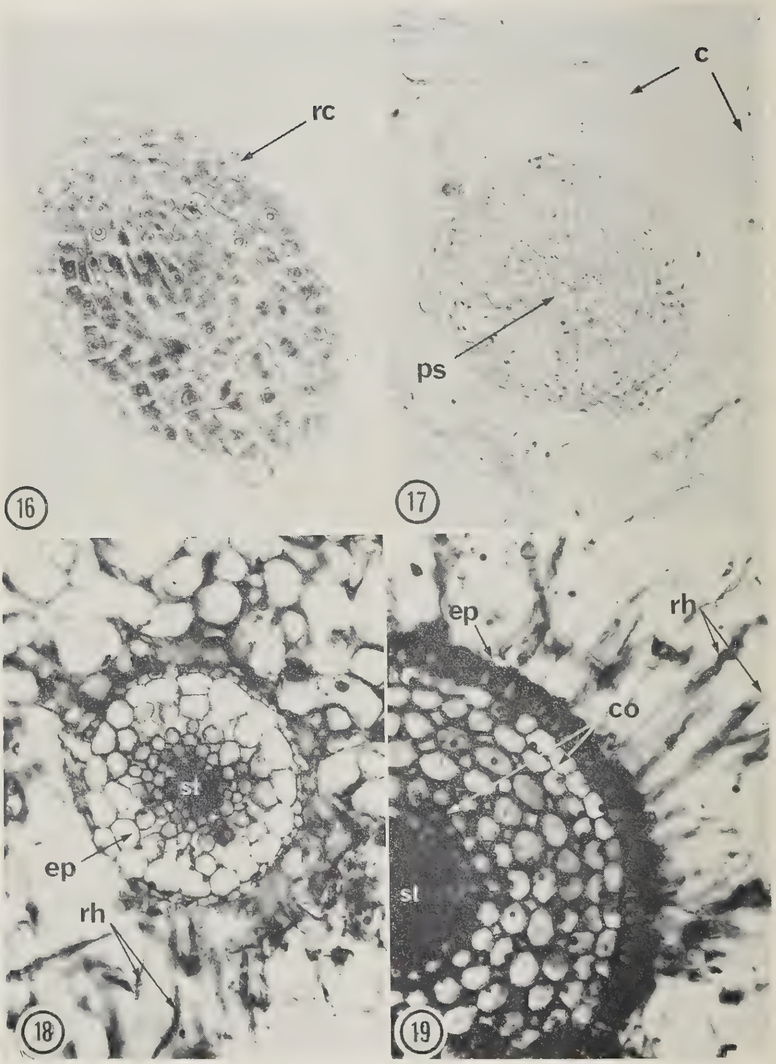
Histogenic and Organogenic differentiation. Most young culture colonies form well-defined cambia and it is from here that vascular structures are organised. These commence with the differentiation of islets of xylem around solitary or small groups of tracheids. Initially, cells surrounding these tracheids develop into rows of flattened cells that probably constitute a cambium, and ultimately result in the formation of cyclic nodules of vascular tissue, the composing elements of which often exhibit radial arrangement. High concentrations of auxin (4·0 mg/l IAA) produced large numbers of tracheids whereas high concentrations of cytokinin (1·2 mg/l kinetin) produced densely compacted xylem tissue.

In our experimental material the path of the vascular bundles could not be determined externally and properly oriented sections were extremely rare. However, as indicated in Figs. 11–12, phloem is a normal structure formed *in vitro* although it was not found associated with the islets of xylem.

Figures 13–15 show three successive stages in the organisation of a shoot. In roots a stele, cortex, and epidermal layer are soon formed immediately behind the meristematic apex deep in the callus (Figs. 16–19). The incidence of root formation in treatments of high auxin and low cytokinin was relatively frequent, ca. 65 per cent. However, a study of their ontogeny is not easy since they are initiated deep within the callus body and not in close association with any discernible structures. Young roots were often located in the callus and when retraced were found to disappear in the undifferentiated callus body. This is contrary to the observations of Steward, Mapes and Mears (1958) who found external roots associated with vascular strands in the callus.

Emergent roots frequently traversed up to 4 cm of callus tissue and when growing out through the callus the root cap behaved much as it would in soil. Root hairs (Fig. 18) were found to grow into the intercellular spaces of existing callus parenchyma. In the air space above the agar as well as in the agar itself root hairs were exceedingly numerous, each epidermal cell probably producing one. Near the apex, behind the root cap, the stele was found to be diarch but further back it is often triarch or polyarch. A frequent anomalous feature was the presence of "Siamese twins", two steles, reminiscent of *Selaginella*, enclosed within one epidermis. Three and even four steles were frequently observed, some with diarch and others with triarch steles. Eventually the steles branch out in dichotomy, each with its own root cap. Roots were often negatively geotropic.

As the cytokinin : auxin ratio increased the formation of roots, unorganised cellular proliferation, and the formation of shoots progressively increased in this sequence. Morphologically, like root meristems, shoot buds resulted from the dedifferentiation of the parenchymatous ground tissue formed by the cambium-like meristem at the surface (Fig. 13), followed by rapid division to



FIGS. 16–19.

Transverse sections through developing roots. IAA:CK, 4·0:0·08 mg/1. Fig. 16.Root. cap region. ×400. Fig. 17. Root, with polyarch stele, embedded in callus. ×160. Fig. 18 Root in callus. Note root hairs growing between cells of callus. ×160. Fig. 19. Tissue zones of root, showing numerous, long root hairs in callus. ×160. Figs. 18–19. Freehand sections of fresh tissue, aniline blue stain.

c, callus; co, cortex; ep, epidermis; ps, polyarch stele; rc, root cap; rh, root hair; st, stele.

form the meristematic bud primordia. Very early in the development of a bud an epidermis was formed from which enormous multicellular trichomes (up to 6·5 mm long) developed. Stomata often developed on the bases of trichomes on young buds. Not infrequently, shoots countered gravity and grew into the agar. Rather striking differences were observed in respect of shoot development when compared with the essential stages of organ initiation as reported by Steward *et al.* (1958). It must be kept in mind, however, that Steward *et al.* worked with liquid media. For example, specific areas with either root or shoot apices were not observed and seldom was there any vascular connection between the callus and even well-formed shoots.

Conclusion

Certain ontogenetic processes observed in cultured tissues are comparable to those in the intact plant. The organisation of a cambium between two tissues of different type is found both *in vitro* and in intact organs. However, the parenchymatous proliferation in cultured tissue is extremely rare in intact plants, and is limited, for example, to the formation of galls and tubers.

Tissue colonies appear to follow a regular and repeatable sequence of stages from their initiation to final completed development. The final form is governed to a large degree, if other factors such as light, temperature and carbon source are constant, by the ratios and concentrations of plant growth regulators supplied through the nutrient media.

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DEVELOPMENT OF NUCELLAR PLANTS FROM UNPOLLINATED AND UNFERTILISED OVULES OF THE WASHINGTON NAVEL ORANGE *IN VITRO**

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Short Communication

Abstract

Previously, pollination and fertilisation have been regarded as essential prerequisites for the initiation of nucellar embryoids in *Citrus*. However, a recent attempt at inducing embryoids and the subsequent differentiation of entire plants from nucellar isolates of ovules of the Washington navel orange has been successfully carried out for the first time.

The induction of pseudobulbils and the subsequent differentiation of embryoids was most effective on a basal nutrient medium supplemented with 40 mg/l adenine and 400 mg/l malt extract. Then, entire plantlets were differentiated from these embryoids when transferred to a basal medium containing 1 mg/l gibberellic acid.

Uittreksel

ONTWIKKELING, *IN VITRO*, VAN NUSELLUS PLANTE UIT ONBESTUIFDE EN ONBEVRUGTE SAADKNOPPE VAN DIE WASHINGTON NAVELLEMOEN. Tot op hede is bestuiwing en bevrugting as noodsaaklike voorvereistes beskou vir die daarstel van nusellêre embrioïede in *Citrus*. Die eerste suksesvolle poging om embrioïede te induseer, gevolg deur differensiasie van volledig ontwikkelde plante uit die nusellêre isolate van die saadknoppe van die Washington nawellemoen, word beskryf. Die induksie, eerstens, van sogenaamde skynbolle en die differensiasie van die embroïede is verkry op 'n basiese voedingsmedium met toevoeging van 40 mg/l adenien en 400 mg/l moutekstrak. Heel plantjies is daaropvolgens uit dié embrioïede gedifferensiëer deur laasgenoemde oor te plant op 'n basiese medium wat 1 mg/l gibberelliensuur bevat het.

Introduction

In addition to meristem culture, the culture of haploid plants from anthers (Guha and Maheshwari, 1967), and cell hybridisation by protoplasmic fusion (Nickell and Torrey, 1969), the establishment of clonal plants of nucellar origin holds great potential significance for crop improvement. *Citrus* nucellar-lines are virus-free, more vigorous, usually higher-producing, and are longer-lived than the parent-line trees although their genetic constitutions, except possibly for occasional somatic mutations, are identical.

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Normally, the Washington navel orange is completely seedless. This results from degeneration of (a) the microsporogenous tissue before the first meiotic divisions occur (Webber, 1894, 1930; Osawa, 1912), with the result that no pollen whatsoever is formed, and (b) the megasporocyte or the megagametophyte (Osawa, 1912). Occasional seeds, 10 in over 25,000 fruits (Shamel, 1918), may be formed as a result of cross-pollination but this rarely occurs as *Citrus* pollen is strictly entomophilous.

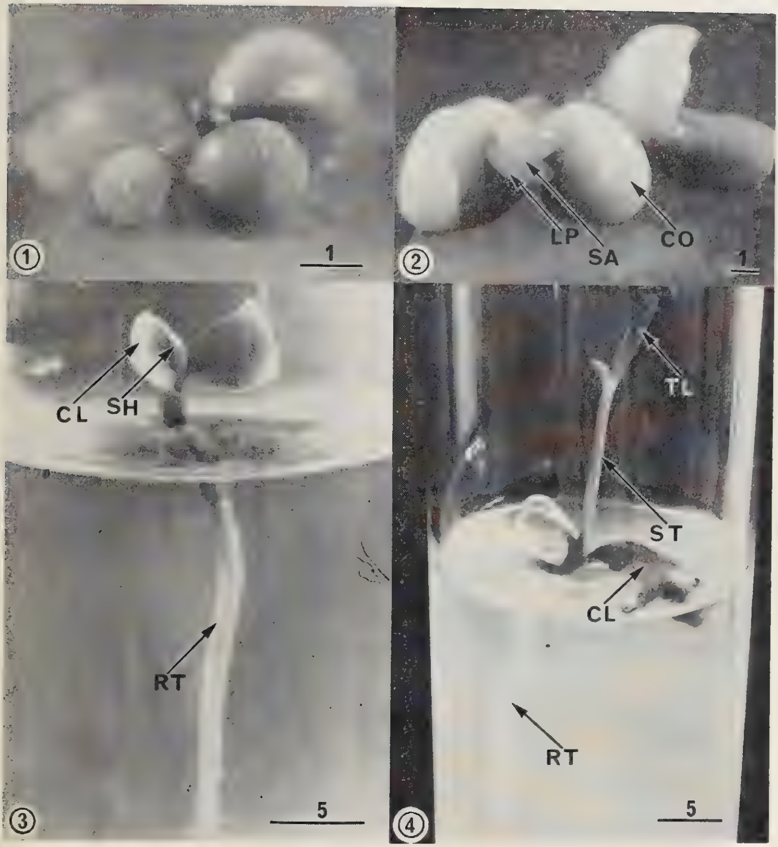
Frost and Soost (1968) concluded that pollination and fertilisation are *usually, but perhaps not invariably necessary* for the initiation of nucella embryos, *in vivo*. Pollination and fertilisation appear to provide an essential stimulus to the nucellus via the zygotic embryo, inducing it to produce adventive embryos. Once this triggering stimulus has been received by the nucellus it appears that the subsequent abortion of the zygotic embryo does not affect further development of the nucellar embryos.

Numerous attempts have been made to culture, and induce differentiation of ovules, zygotic embryos, and nucellar embryos of *Citrus in vitro* (Stevenson, 1956; Ohta and Furusato, 1957; Rangaswamy, 1958a, 1958b, 1959, 1961; Rangan, Murashige and Bitters, 1968, 1969). Sabharwal (1962) was unable to induce development of nucellar embryos *in vitro* unless these had been initiated before excision of the nucelli. The inference here of the necessity for a prior stimulus, was supported more recently by Rangaswamy (1970) who is of the opinion that pollination and fertilisation are essential prerequisites for the initiation and development of nucellar embryos *in vitro*. Rangan *et al.* (1968, 1969) are the only workers who have succeeded in triggering the initiation of adventive embryos in the nucellus of some monoembryonic *Citrus* varieties. They used excised nucellar isolates from developing seeds which had been fertilised with compatible pollen of *Poncirus trifoliata*.

As far as could be ascertained, nucellar embryoids have never been successfully initiated and differentiated from unfertilised, unpollinated ovules where no adventive embryos had been stimulated. Considering the advantages of producing nucellar plants from unpollinated, unfertilised ovules, particularly of monoembryonic cultivars, a series of experiments were undertaken in an attempt to initiate such plants by the careful control and manipulation of basal nutrient media, hormones, and other plant growth regulating substances.

Materials and Method

Fruits were picked from a Washington navel orange tree at the Ukulinga Research Station, Pietermaritzburg, about eight weeks after anthesis. Careful microscopic examination indicated that the ovules showed no signs of either zygotic or adventive embryo development. Nucellar isolates, ca. 0·1 mm^3,



FIGS. 1—4.
Stages in development of plantlet from nucellus of unpollinated ovule of Washington navel orange. Fig. 1. Pseudobulbils, 30 days after transfer of nucellar isolates to culture medium containing 40 mg/1 adenine and 400 mg/1 malt extract. Fig. 2. Differentiated embryoids at 60 days. Fig. 3. Germinating embryoid, 10 days, after transfer to culture medium containing 1 mg/1 gibberellic acid. Fig. 4. Entire plant, 28 days after transfer. CO, cotyledon; CL, cotyledonary leaf; LP, leaf primordium; RT, root; SA, shoot apex; SH, shoot; ST, stem; and TL, true leaf. Scale lines in mm.

were excised aseptically with the aid of a dissecting microscope and placed on a basal nutrient medium (BM) composed of the inorganic salts of White (Rangaswamy, 1961) or Murashige and Skoog (1962). The following organic substances were added (in mg/1):

glycine, 5·0; thiamine hydrochloride, 0·3;
pyridoxin hydrochloride, 0·05; niacin, 1·0;
calcium pantothenate, 0·03; myo-inositol, 100;
sucrose, $4 \cdot 0 \times 10^4$; and agar, 10^4

The pH of the complete medium was adjusted to 5·6 before autoclaving for 15 minutes at 1·05 kg/cm^2.

Plant growth substances. From extensive work in progress in our tissue culture laboratory on the monoembryonic varieties—Ellendale mandarin and Shaddock, various types, concentrations, combinations, and ratios of auxins, cytokinins and gibberellins were used, and it became clear that these plant hormones, *per se*, do not stimulate the nucellus into forming embryoids. Other organic additives used in these experiments included yeast extract, coconut milk, malt extract, ascorbic acid, casein hydrolysate, adenine and adenine sulphate.

The only additives which showed promise were coconut milk, adenine, adenine sulphate, ascorbic acid and malt extract and it was therefore decided to test their efficacy, alone and in combination, in inducing embryoids in nucellar isolates of unfertilised and unpollinated Washington navel ovules at the following levels:

coconut milk (CM), 15% v/v; adenine (AD), 40 mg/1;
adenine sulphate (AS) 40 mg/1; ascorbic acid (AA), 40 mg/1;
and malt extract (ME), 400 mg/1.

Culture conditions. The nucellar isolates were cultured in test tubes fitted with Cap-O-Test caps lined with non-absorbent cotton wool and held at 24 ± 2°C under a photoperiod of 16 hours. Light was supplied from Gro-Lux fluorescent tubes at an intensity of 10^3 lux.

Results and Discussion

Initiation and development of nucellar embryoids. Rangan *et al.* (1968, 1969), working with fertilised ovules, reported a response in nucellar embryoid initiation from a medium which included either the auxin, napthaleneacetic acid, in combination with orange juice and adenine sulphate, or malt extract only.

Embryoids have been induced of course, in free-cell cultures as well as from tissue explants taken from many plant organs but the necessity and role of substances such as casein hydrolysate, auxins, and coconut milk in the induction and differentiation of embryoids is still not clear (Konar and Nataraja, 1965a, b; Johri and Sehgal, 1966; Sussex and Frei, 1968).

The first signs of growth in our nucellar isolates were the appearance of *pseudobulbils* (Fig. 1), a term used by Rangaswamy (1958a). These were first observed about 4 weeks after transplanting, being preceded by very little callus formation. Pseudobulbils gradually developed into embryoids (Fig. 2). Although

there is inconsistency in the literature, an 'embryoid' is generally accepted as being an organ similar in structure to an embryo but derived asexually. No growth occurred on BM alone, and occurred to a limited extent only on BM + AA. However, when on BM + AD or BM + AS or BM + ME, growth was rapid with numerous embryoids developing from the pseudobulbils. Basal medium + CM was not as effective, but when used in combination with AD, AS and/or ME, it did increase the incidence of pseudobulbil and embryoid formation. Basal medium + AD + ME yielded the best results by not only initiating the largest number of pseudobulbils but also by producing most embryoids per nucellar isolate. Further differentiation of the embryoid masses into discrete organs at this stage—about 10 weeks—appeared impossible on any of the above media.

Differentiation of embryoids and development of plantlets. We did not wish to assume that because the plant hormones auxin, cytokinin and gibberellin had no apparent effect on embryoid initiation in the nucellar isolates, they would be equally ineffective in inducing the differentiation of complete organs, despite the fact that Steward (1969) had shown that auxin prevents differentiation of entire plants from embryoids in some free-cell cultures.

Consequently, the embryoid masses were subdivided and, as far as was possible, only single embryoids were transferred to the following media:

BM + 0·1 mg/l indoleacetic acid (IAA);
BM + 0·1 mg/l kinetin (CK); and BM + 1·0 mg/l
gibberellic acid (GA_3)

Gibberellic acid was included since in previous experiments we had found it to promote the formation of roots. This was somewhat unexpected since GA_3 is not generally associated with root initiation. Rangaswamy (1961) did, however, find a similar response in his nucellar cultures. Within one week of transplanting the embryoids more than 60 per cent on BM + GA_3 had developed roots (Fig. 3). No roots were formed in the other treatments until about three weeks after transplanting, and then only in a limited number.

The emergence of the first true leaves occurred about three weeks after transplanting (two weeks after the radicle appeared), but only in plantlets on BM + GA_3 (Fig. 4). At the time of writing (four weeks after transplanting) BM + GA_3 is still the only medium on which entire plantlets have been formed. It is possible, however, that entire plantlets will be formed on BM + IAA and BM + CK. But it is doubtful whether any will be formed on BM alone as further slow generation of embryoids is occurring.

Isolated, single embryoids differentiate more readily than aggregates following transplantation.

Conclusion

What appears to be the first successful attempt at producing nucellar citrus plants from unpollinated and unfertilised ovules, has been achieved in our laboratory. An important practical application of this technique is that it can be used to import seedless citrus varieties without the danger of introducing new viral diseases, thus obviating the necessity of subjecting vegetative material to long periods of quarantine. In addition, it can be used to rapidly propagate a large number of clonal nucellar trees from say a single fruit of a seedless *Citrus* variety since numerous embryoids and plantlets can be differentiated and grown from each original nucellar explant.

We are at present attempting to induce embryoids in the nucellus of unpollinated, unfertilised ovules of the Ellendale mandarin, a monoembryonic variety of commercial importance in South Africa.

We are also attempting to find and identify the active fraction of ME, and are carefully testing the efficacy of AD and AS, since AD appeared to be more effective even when the equivalent amount of AD was applied in the sulphate form.

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Statistics and Experimental Design by Geoffrey M. Clarke, with pp. xi + 161. London: Edward Arnold (Publishers) Ltd., 1969. 42/- (£2.10p).

This book is written for biologists by an author with considerable experience of working with research biologists and teaching students of biology. At the same time, the general principles of elementary statistics covered by the text will be of interest to non-biologists. This is a comparatively low priced text in the Contemporary Biology Series edited by Professors Barrington and Willis. It consists of 136 pages of text divided into seventeen chapters, one page of references and bibliography, twelve pages of answers to and comments upon exercises, and an index in two parts—one to statistical terms and the other to topics used as examples.

This small text is an admirable introduction to statistics for the non-mathematical student in his second year at a South African university. The book begins by defining population, samples and variates and illustrating methods of summarising data by means of charts. The concept of probability is, as usual, introduced through the Binomial Distribution. This is followed by a consideration of the Poisson and Normal Distributions. Other tests of significance fully dealt with are the distributions based on Students t, Chi-squared and F. Linear regression and the Analysis of Variance are briefly touched on in Chapter II. However, subsequent chapters dealing with Experimental Design introduce the reader to the practical application of the Analysis of Variance in considerable detail. The importance of experimental design and the conditions that must be satisfied before an analysis of variance is undertaken, are as one would expect, properly stressed and the ways by which they may be attained are described.

Each chapter contains suitably worked examples chosen from the wide field of experimental biology and at the end of each chapter, exercises are given. This enables a student to use the book independently of a tutor and obtain a clear insight into elementary statistics, particularly by working out the exercises and checking his conclusions with the answers and comments at the end of the book.

This book is recommended to all interested in the application of statistics to problems in the fields of agriculture, plant physiology, ecology, entomology, genetics, cytology and microbiology.

E. S. Twyman

The Systematic Identification of Flavonoids by T. J. Mabry, K. R. Markham and M. B. Thomas, with pp. xi + 354. Berlin: Springer-Verlag, 1970.

A text of this nature is long overdue, and Professor Mabry, with some twenty papers relating to studies into the flavonoids of *Baptisia spp.* emerging from his school in Texas since 1965, is highly qualified to have undertaken this task. The book is arranged in three clearly defined parts: Part I—the isolation, purification and preliminary identification of flavonoids; Part II—the structure analysis of flavonoids by ultraviolet spectroscopy; Part III—the structure analysis of flavonoids by proton nuclear magnetic resonance spectroscopy. These parts indeed combine to achieve the objective of the book. Though the field is specifically limited to the flavones, flavonols, flavanones, flavanonols, isoflavones, chalcones and aurones as well as their glycosides, it is nevertheless treated in great detail both in the practical aspects and in the interpretation of the results. In Part I for example, full details are given for the construction of a simple chromatography cabinet and for the preparation of polyamide for column chromatography. Owing to their greater stability, tertiary butyl alcohol chromatographic solvents are preferred to the conventional l-butanol systems. In Part II, full details on the methods employed in obtaining UV spectra are presented and the interpretation of the spectra is thoroughly discussed with ample illustrations. The inclusion in this Part of comprehensive data relating to the chromatographic and UV spectral properties as well as spectral charts of 175 flavonoids enhances the practical value of this book. In Part III, the techniques used to prepare compounds for NMR analysis, particularly as their trimethylsilyl ethers, and the interpretation of the NMR spectra are described in detail. This part, like the preceding one, concludes with full NMR spectra of 125 flavonoids as their TMS ethers.

As a whole the book is clearly and attractively presented with remarkably few errors. The reviewer found one spelling error (p. 16, line 3 from the bottom should read "may" for

"many") and one printing error (in Table V-1 on p. 42, should have ref. "*b*" for "*a*" next to Morin). More pedantic readers would prefer the term "aqueous ammonia" for "ammonium hydroxide" (p. 7, line 1) and in the formulae on pp. 8 and 9, the symbols R^1 and R^2 for R_1 and R_2 respectively. The only serious fault is the omission of the numbering of the pages which contain the UV spectra. However there is an erratum sheet which must be consulted in conjuction with the subject index when one wishes to locate the UV spectra of a particular flavonoid.

These criticisms, however, become insignificant in comparison to the value of the book which has unquestionably achieved its objective. This book deserves a readily accessible place among the reference books in any laboratory engaged in the chemistry of plant products.

J. F. Elsworth

Plant Structure and Development: A Pictorial and Physiological Approach by T. P. O'Brien and M. E. McCully, with pp. viii + 114, figs. 155. Macmillan, 1969. £5.

This is an unconventional and interesting book. The sub-title is misleading in that the treatment of structure is hardly more physiological than is nowadays customary. On the other hand a pictorial approach can too often be equated with superficiality, which, taking the book as a whole, is not a criticism which can be made here. The plan followed consists of a summary of contemporary views of the structure and development of the plant cell, shoot apex, root, stem, leaf, reproductive tissues and seeds. The reader is directed to further study by the provision of carefully selected, up-to-date and readily available references.

It should be pointed out that, contrary to the suggestion in the preface, this is not a book for beginners. The text is concise to the point of brevity, although the numerous illustrations form an integral part of the narrative. However, the discerning reader will find that many established ideas are presented in a new light and that there is much that is provocative.

A commendable feature is the specification of the methods of preparation of the material upon which the illustrations are based. Much use is made of excellent electron-micrographs, and of photomicrographs based on the techniques of Feder & O'Brien. The histochemical approach is interesting but one would wish for a more comprehensive statement of the significance of the PAS and toluidine blue staining reactions. Many of the photomicrographs are very good but the imposed limitation of techniques has resulted in some which are definitely inferior, such as those of the stem apex, micro- and mega-gametogenesis.

Lastly, it is improbable that this book would be bought for the coffee table. The lavish style of production is therefore unnecessary and the equivalent of 18 pages which are either blank or bear only a chapter heading and a botanical embellishment would have been better utilised in the expansion of the text.

A. R. A. Noel

INSTRUCTIONS TO CONTRIBUTORS TO THE JOURNAL OF SOUTH AFRICAN BOTANY

This Journal provides a medium for the publication of the results of botanical research primarily on the flora of Southern Africa, whether systematic, morphological, ecological or otherwise and whether carried out in South Africa or elsewhere. Papers on botanical subjects of special interest and application in South Africa may be included.

Contributions must be original and should not be translations of previously published papers.

Papers must be submitted in final, corrected form. They are accepted for publication on the recommendation of the Editorial Committee.

Authors may be charged expenses for corrections if alterations are excessive.

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Papers should be type-written, double spaced throughout on one side of the paper and with margins of at least 3 cm (1 inch). Footnotes and elaborate tables should be avoided. Latin binomials should be underlined once to indicate italics. All other marking of copy should be left to the Editor. The original, plus at least one carbon copy, must be submitted.

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Each paper should be headed with a concise informative **title** in capitals with the author's name below. This should be followed by the name of the institution, where the work was carried out, underlined and placed within brackets.

A concisely written **abstract** in English and Afrikaans, of not more than 200 words, should precede the text.

The subject matter should be divided into sections under short appropriate **headings** such as: INTRODUCTION, MATERIAL AND METHODS, RESULTS, DISCUSSION, CONCLUSION, ACKNOWLEDGMENTS, etc.

Tables and **illustrations** should be on separate sheets. **Figures** and **graphs** should be in Indian ink on white card or Bristol board. Lettering for figures can be inserted by the printers in which case authors should indicate the desired lettering on the original figure lightly in pencil. The maximum dimensions available for figures are 18 cm $\times$ 12 cm ($7'' \times 4\frac{1}{2}''$). Line drawings for blocks should be at least twice the size they will be when reduced for publication. All figures should be supplied with a scale. The most suitable method of indicating magnification is a scale line (in metric units) incorporated in the figure. Photographs for half-tone reproductions should be on glossy paper, clearly marked on the reverse side (in pencil) to indicate the top. Line drawings and half-tone illustrations are termed figures and should be numbered consecutively. Captions for figures should be typed on a separate sheet of paper.

TAXONOMIC PAPERS

Authors must adhere to the International Rules of Botanical Nomenclature. **Abbreviations of herbaria** must be cited in accordance with the most recent edition of Index Herbariorum, Pt 1 (The Herbaria of the World, 5th ed., 1964). When **new species** are described, the exact location of type material must be indicated. When proposing **new combinations** the full citation of the basionym is required. **Indented keys** with numbered couplets are preferred when dealing with a small number of taxa. **Bracket keys** should be used when dealing with a large number of taxa. When citing **synonyms** they should be arranged chronologically into groups of nomenclatural synonyms and these should be

arranged chronologically by basionyms. Whenever possible, the types of the basionyms should be cited, e.g.:

Bequaertiodendron magalismontanum (Sond.) Heine & J. H. Hemsley in Kew Bull. **1960**: 307 (1960).
Chrysophyllum magalismontanum Sond. in Linnaea **23**: 72 (1850). Type: Magaliesberg, *Zeyher,* 1849 (S, holo; BOL!, SAM!).
Zeyherella magalismontana (Sond.) Aubrév. & Pellegr. in Bull. Soc. bot. Fr. **105**: 37 (1958).
Pouteria magalismontana (Sond.) A. Meeuse in Bothalia **7**: 335 (1960).
Chrysophyllum argyrophyllum Hiern, Cat. Afr. Pl. Welw. **3**: 641 (1898). Syntypes: Angola, *Welwitsch* 4827, 4828, 4829 (BM!).
Boivinella argyrophylla (Hiern) Aubrév. & Pellegr. in Bull. Soc. bot. Fr. **105**: 37 (1958).
Chrysophyllum wilmsii Engl., Mon. Sapot. Afr.: 47 t. 16 (1904). Type: Transvaal *Wilms* 1812 (B†, holo.; K!).
Boivinella wilmsii (Engl.) Aubrév. & Pellegr. in Bull. Soc. bot. Fr. **105**: 37 (1958).

CITATION OF SPECIMENS

In the interests of uniformity contributors are requested to follow the recommendations of the Botanical Research Institute, Pretoria (Technical note: Gen. 4, Oct., 1967) by citing specimens according to the one degree grid system. Distribution data are given separately for each province and are arranged in the following sequences: South West Africa, Botswana, Transvaal, Orange Free State, Swaziland, Natal, Lesotho, Cape. Within each province degree squares are listed in numerical sequence, i.e., from west to east and from north to south. Whenever possible locality records should be given to within a quarter degree square. The collectors' names and numbers are underlined (printed in italics) to avoid confusion with the numbers of the degree squares, e.g.: NATAL—2829 (Harrismith): Cathedral Peak Forest Station (-CC), *Killick 1527* (PRE); . . . CAPE—3418 (Simonstown): Hottentots Holland mountains, Somerset Sneeukop (-BB), Nov., *Stokoe s.n.* sub. SAM *56390* (SAM).

REFERENCES

These should be given in the text as follows: Jones (1968) or (Jones, 1968) or, where reference to a specific page is required, Jones (1968:57) or (Jones, 1968:57). **Literature cited** should be arranged alphabetically by surnames, chronologically within each name, with suffixes a, b, etc., to the year for more than one paper by the same author in that year. Titles of **periodicals** must be abbreviated according to the *World List of Scientific Periodicals,* 4th ed., London: Butterworth or when unable to trace the title in this list (as will be the case in taxonomic papers where abbreviations of 18th and 19th century periodicals are required) the abbreviations given in *Botanico-Periodicum-Huntianum,* Pittsburgh: Hunt Botanical Library, 1968, should be followed. Periodical titles should be underlined once (for italics). If an author is unable to determine the correct abbreviation of a journal title he is advised to type it out in full and leave its abbreviation to the Editor. Titles of **books** should be underlined and given in full, together with the place of publication, name of the publisher and an indication of the edition if other than the first; e.g.:

Davis, P. H. and Heywood, V. H., 1963. *Principles of Angiosperm Taxonomy.* Edinburgh and London: Oliver and Boyd.

Riley, H. P., 1960. Chromosome numbers in the genus *Haworthia. Jl S. Afr. Bot.* **26**: 139—148.

Jl S. Afr. Bot. 37 (3): 139–142 (1971)

SOMATIC CHROMOSOMES OF *NERINE ANGUSTIFOLIA* AND *N. PLATYPETALA*

J. B. Gouws

(*University of Western Cape*)

Abstract

The somatic chromosomes of two *Nerine spp.* have been investigated. Each has 22 somatic chromosomes. Morphological differences were observed between the f and g chromosomes of the two species. The other chromosomes correspond very closely, suggesting a close relationship.

Uittreksel

SOMATIESE CHROMOSOME VAN *NERINE ANGUSTIFOLIA* EN *N. PLATYPETALA*

Die somatiese chromosome van twee *Nerine* soorte is ondersoek. Elk het 22 somatiese chromosome. Morfologiese verskille is waargeneem tussen die f en g chromosome van die twee soorte. Die ander chromosome toon 'n groot ooreenkoms wat op 'n noue verwantskap dui.

Materials and Method

Bulbs of the two *Nerine species* were obtained from Mr. Gordon McNeil of Dindinnie, Northern Transvaal. These were potted in sand, placed in a shade house and regularly watered with tap water for a period of two months. The plants were then removed from the pots and soaked in tap water to dislodge all sand particles. The young roots were immediately decapitated and the tips immersed for 2 hours in a $\frac{1}{2}\%$ Colchicine solution as recommended by Darlington, and la Cour (1962). The root tips were then fixed overnight in Carnoy prepared according to Johansen (1940) 2nd formula. They were then macerated in $\frac{N}{10}$ HCl and stained in acetic ocrein Darlington, la Cour (1962) for two hours. The excess stain was washed off in a 10% acetic acid solution, squash preparations were made, these were ringed with Canada balsam and immediately inspected.

Drawings were made at table level by means of a Zeiss standard microscope with 100X oil immersion plan objective and drawing tube.

Results

Nerine angustifolia, 22 somatic chromosomes. Fig. 1 a and b. The single pair of long chromosomes are V-shaped with a sub-median constriction and little difference between the length of the two arms. The next 6 pairs, b–g, form a graded series from medium sized with a sub-terminal to a sub-median constriction. The proximal arms of chromosomes b, c and d are approximately

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Fig. 1a.
Nerine angustifolia.

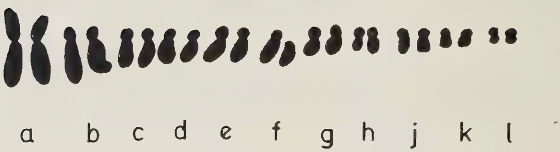

Fig. 1b.
N. angustifolia.

the same size, but each pair is distinct as the distal arms vary in length from the b pair where these are as long as the longer arms of the a pair, to the comparatively short arms of the d pair. The e and f pairs could not be distinguished from one another. They are approximately the same size as the c pair, but distinct from these as their proximal arms are slightly longer. The g and h chromosomes are short with sub-median constrictions but the g pair is slightly longer than the h pair. The h and j pairs again resemble each other very closely as far as the total lengths and the positions of the centromeres are concerned. They could not be distinguished with much certainty from one another. The k and l pairs are almost microchromosomes with the 1 pair the smaller of the two. In fact the two arms are each a small ball with a diameter less than the width of one of the other chromosomes.

Nerine platypetala, 22 somatic chromosomes. Fig. 2 a and b.

The chromosomes of this complex are, on the whole longer than those of *Nerine angustifolia*, but this may be due either to a less advanced metaphase or a

slightly shorter Colchicine action. Morphologically the karyotype is much like that of the previously discussed species. The differences observed are the following:

(1) The f chromosomes of *Nerine angustifolia* are J-shaped while those of *N. platypetala* are V-shaped.

(2) The g chromosomes of *N. platypetala* have a secondary constriction in the distal arm with a trabant almost the size of the proximal arm.

The other chromosomes of the two karyotypes are almost identical.

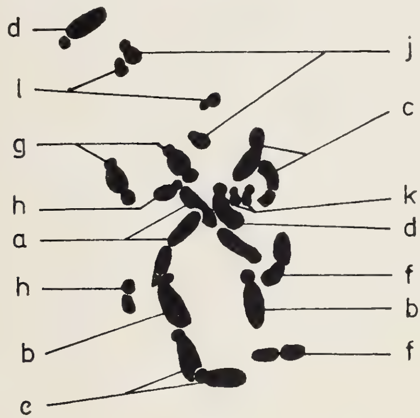

FIG. 2A.
Nerine platypetala.

FIG. 2B.
N. platypetala.

DISCUSSION

Apparently the two species have been investigated cytologically for the first time. The 22 somatic chromosomes occur repeatedly in the genus Nerine. Occasionally there seems to be a variation in the number of the short chromo-

somes cf. Gouws (1949), Heitz (1926) and James and Addicot (1941) and Inariyama (1937). However, the prevalent number seems to be 2n = 22. The karyotypes of the present two species, besides showing a reasonable degree of similarity with those previously investigated, show also a very marked correspondence between their chromosomes except for the f and g pairs as reported above. This seems to show that *N. angustifolia* and *N. platypetala* are closely related but the karyological evidence supports the view that these are distinct species.

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DIE „POTCH" BOOMMETER

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UITTREKSEL

'n Apparaat wat op 'n eenvoudige beginsel gebasseer is, waarmee die hoogte, kruindeursnee en stamdeursnee van bome eenvoudig en redelik akkuraat bepaal kan word, is gedurende 1967–68 aan die Potchefstroomse Universiteit ontwikkel en gebou.

ABSTRACT

THE POTCH TREE METER

A relatively simple instrument for the measurement of dimensions of trees and bush was developed and built at the University of Potchefstroom.

Alhoewel daar verskeie ekologiese metodes bestaan waarvolgens die dimensies van bome bepaal kan word, bly daar steeds 'n sterk behoefte vir verbeterde opnametegnieke en doeltreffender apparaat.

'n Apparaat, wat op 'n eenvoudige beginsel gebasseer is, en waarmee die kruindeursnee, hoog teen stamdeursnee van bome eenvoudig en redelik akkuraat bepaal kan word, word hier kortliks toegelig. Die apparaat is gedurende 1967–68 deur die skrywers ontwerp en deur die instrumentmakery van die P.U. vir C.H.O. gebou.

Dit bestaan uit 'n ligte metaalhouer wat ongeveer 4 cm hoog en 19 cm lank is. Die voorkant van die houer is 23 cm breed terwyl dit agter 6 cm breed is. Die agterste wand is van 'n gleuf van 1 × 3 cm voorsien terwyl die voorste wand heeltemal deursigtig is en daar gevolglik deur die houer gekyk kan word. Binne in hierdie houer, is twee vertikale plate (5 cm uit mekaar) op so 'n wyse aangebring dat hulle op vaste punte aan die agterkant kan skarnier. Die voorpunte wat effens na binne gebuig is, is aan 'n gesinkroniseerde stelskroef verbind sodat die voorste punte van die plate deur die verstelling van die skroef verder weg van, of nader aan mekaar beweeg kan word. Op hierdie wyse kan die gesigsveld deur die houer dus vergroot of verklein word. 'n Perspeks-skyf met 'n skaalindeling (voete) is aan die stelskroef bevestig, terwyl 'n ander skaalindeling (jaart) onder die perspeks-skyf op die bokant van die houer aangebring is. Lesings word geneem deur op 'n geskikte afstand (5, 10, 15, 20, 25 of 30 jaarts) van 'n boom te staan, deur die apparaat daarna te kyk en die gesigsveld, horisontaal i.g.v. kruin en stamdeursnee, en vertikaal in geval van hoogte, so te verstel dat die betrokke dimensie die hele gesigsveld t.o.v. die

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verstelbare as vul. Die lesing (dimensie) vir die korrekte dimensie kan dan direk op die perspeks-skyf afgelees word. Die afstand tussen die opnemer en die boom moet vooraf afgetree of d.m.v. 'n afstandmeter bepaal word.

Opmerkings

1. Tydens veldproewe is gevind dat die apparaat verkieslik gesteun moet word wanneer lesings oor lang afstande geneem word aangesien beweging foutiewe resultate veroorsaak.
2. Die apparaat is ontwerp om bome en bosse met maksimum dimensies van 25 m te meet en groter bome of bosgroepe sal derhalwe nie met hierdie model bestudeer kan word nie.
3. Die afstand tussen die lens van die oog en die gleuf van die apparaat beinvloed die lesings tot 'n mate en elke opnemer sal die apparaat volgens sy omstandighede moet instel, of die fout bepaal en korreksies daarvoor moet aanbring.
4. Vir die bepaling van stamdeursnee sal 'n noukeuriger skaalindeling moontlik 'n verdere verbetering wees. Moeite word soms ondervind om te besluit waar die grense van die kruin presies geneem moet word, sodat die voet-skaal hiervoor bevredigend werk.
5. Verskeie geringer veranderings wat die apparaat meer doeltreffend sal maak word tans ondersoek.

Erkennings

Die apparaat is ontwikkel met finansiële steun van die Dept. van Landbou Tegniese Dienste.

THE POTCH TREE METER

Abstract

A relatively simple instrument for the measurement of dimensions of trees and bush, was developed and built at the University of Potchefstroom.

Uittreksel

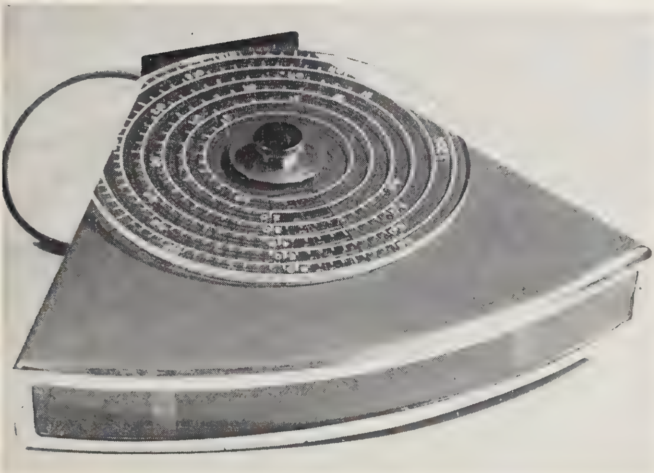
DIE „POTCH" BOOMMETER

'n Apparaat wat op 'n eenvoudige beginsel gebasseer is, waarmee die hoogte, kruindeursnee en stamdeursnee van bome eenvoudig en redelik akkuraat bepaal kan word, is gedurende 1967–68 aan die Potchefstroomse Universiteit ontwikkel en gebou.

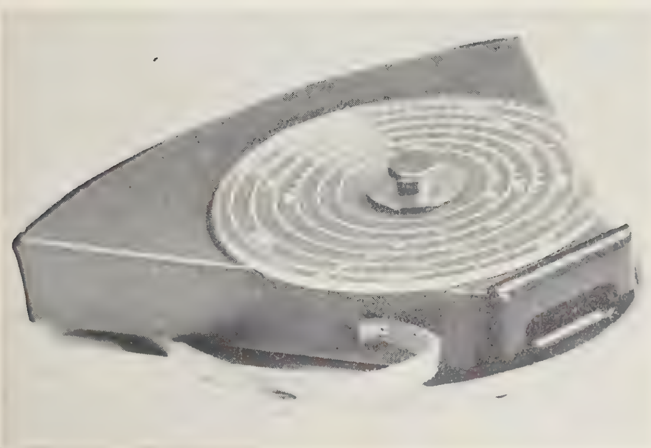
Discussion

The instrument consists of a light metal and perspex body, approximately 19 cm long and 4 cm high, tapering from a width of 23 cm in front to a width of approximately 6 cm at the back.

A horizontal slit (approximately 1×3 cm) at the back, enables objects to be viewed through a perspex window in front. The field of view can be laterally



(a)



(b)

FIG. 1.
„Die Potch" Boommeter. The „Potch" Tree Gauge.
(*a*) View from front.
(*b*) View showing observation slit.

adjusted by turning a control knob, coupled to movable horizontal shutters behind the perspex window. A calibrated perspex disc is attached to the control knob on the upper side of the instrument.

By sighting through the instrument and adjusting the control knob until the object to be measured is delimited by the shutter blades, the appropriate dimension of the object can be read off from the calibrated disc, provided that the distance from the point of observation to the object (i.e. the observation distance) is known.

Remarks

1. The use of a rangefinder to determine the observation distance is recommended.
2. It is advisable to mount the instrument on a tripod when working over long observation distances.
3. An operator should familiarize himself thoroughly with the instrument before field use.
4. The present instrument (Figure 1) may be used for measuring objects with sizes between 0,5 m and 25 m.
5. Certain improvements of the present instrument are being contemplated.

Acknowledgments

The development and building of this instrument was made possible by the financial aid of the Department of Agricultural Technical Services.

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THE MORPHOLOGY AND DEVELOPMENT OF *ANTENNULARIA ENGLERIANA* (P. Henn.) v. Höhn.[1]

S. K-M. Tim and E. S. Twyman

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Abstract

The ascostroma results from the coiling and anastomosing of the superficial hyphae. Pseudoparaphyses arise as outgrowths of cells of the psuedoparenchymatous centrum and are connected to the top and bottom of the locule. Asci grow up between the pseudoparaphyses and centrum development is of the Pleospora type.

Uittreksel

DIE MORFOLOGIE EN ONTWIKKELING VAN ANTENNULARIA ENGLERIANA (P. HENN.) V. HOHN.

Die askostroma ontstaan as gevolg van die opdraai en saamgroei van die oppervlakkige swamdrade. Pseudoparafises ontwikkel as uitgroeisels van die pseudoparenchiem sentrum en is aan die bokant en onderkant van die hokkie van die askostroma geheg. Askusse groei opwaarts tussen die pseudoparafises en die ontwikkeling van die askostroma geskied soos dié van die Pleospora-tipe.

Introduction

Antennularia engleriana is a fungus which is parasitic on the stems of species of *Erica* (Ericaceae). This fungus has been assigned to various genera over the last 70 years. It was perhaps Doidge (1941) who described it most comprehensively under the name *Dimerosporiopsis engleriana*, a combination proposed by Hennings (1901). Von Höhnel (1909) transferred it to the genus *Antennularia* whilst retaining the epithet of Hennings, hence *Antennularia engleriana* (P. Henn.) v. Höhn. In 1928, v.d. Byl proposed a new combination for this fungus, this being *Gibbera engleriana* (P. Henn.) v.d. Byl.

According to the taxonomic characteristics followed by Müller and von Arx (1962), this fungus must be placed among the Venturiaceae on spore characteristics and the presence of an hypostroma. However, the possession of superficial hyphae would preclude its inclusion in the genus *Gibbera* and the fungus has thus been transferred back to *Antennularia* under the original combination of *A. engleriana*. The use of the latter name here is one of convenience. In the light of the lack of detailed developmental studies on genera noted as synonyms for this fungus, it seems futile to debate the validity of the assignation of any particular name. This description is therefore offered purely from a developmental point of view with the object of finding out whether or

[1] Based on a dissertation submitted by one of the authors (S. K-M. T.) to Rhodes University in partial fulfilment for the degree of Doctor of Philosophy.

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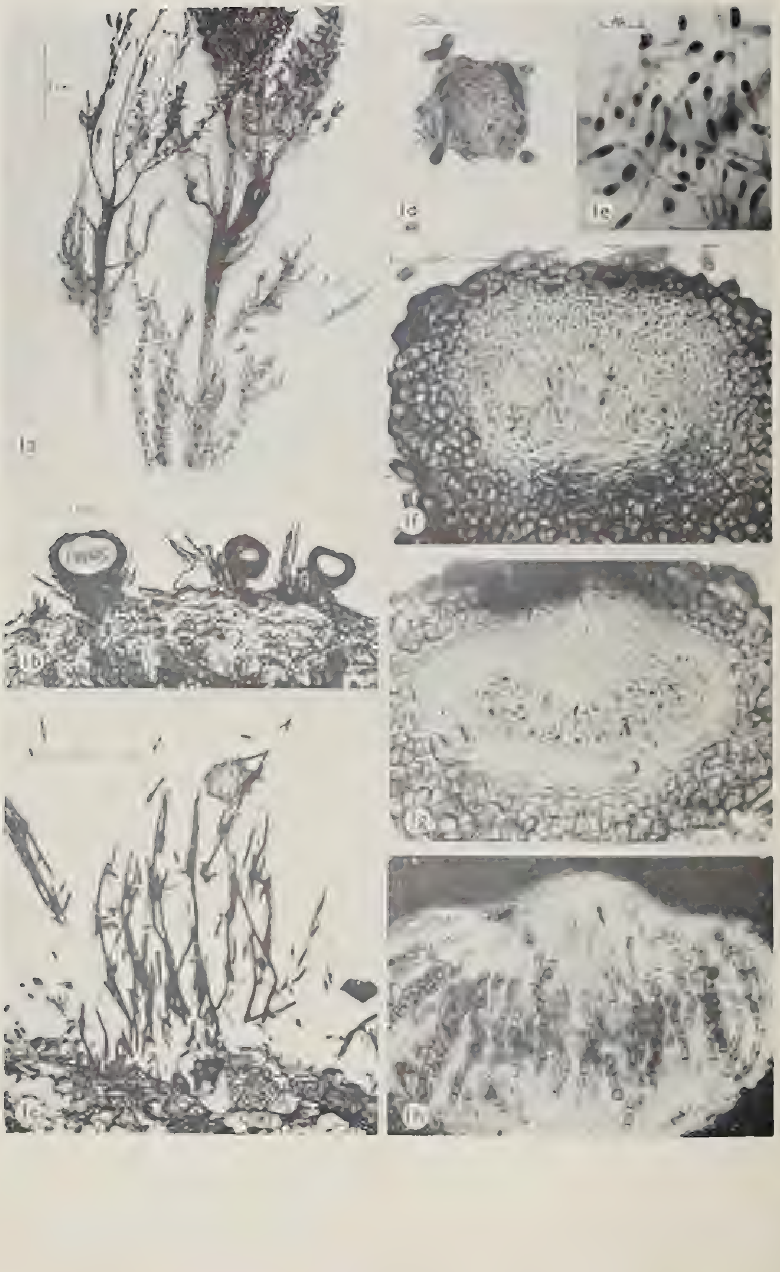

not the formation of the centrum conforms with one of the types proposed by Luttrell (1951) and, on this basis, to suggest its taxonomic position.

Materials and methods

The material for this study was found growing on the stems of *Erica*. Collections of parasitised *Erica brownleea* Bol. were made during April 1965/6 and also in March, 1966 from the Hogsback area (nr. Alice, E. Cape) and of *Erica nemorosa* Kl. ex Benth. in the Belmont Valley, Grahamstown, Cape Province, during November, 1965 and February/March, 1966.

For developmental studies, portions of cortical tissue plus fungus were fixed in formalin-acetic-alcohol, dehydrated in a butyl alcohol series, imbedded in paraffin wax (55°C.) and sectioned at 8μ on a rocker type microtome. For certain sections, a sledge microtome was also employed.

The sections were, in most cases, stained in Heidenhain's haematoxylin and counterstained in Orange G (Johansen, 1940). Temporary squash preparations were made from fresh and fixed material. The early stages of ascocarp formation were deduced from the superficial hyphae mounted in lactophenol but for studies of the pseudoparaphyses, the preparation and staining techniques according to Wittman (1962) were employed. For the investigation of the hypertrophy of the stem, sections were cut in the transverse, radial and tangential planes and stained in safranin and fast green.

Host-parasite Relations

Fungal invasion is initiated on very young shoots of the host plant resulting in the hypertrophy of these areas (Fig. 1A). The peridermal areas become cracked and the entire area is covered with a brown to black mass of inter-

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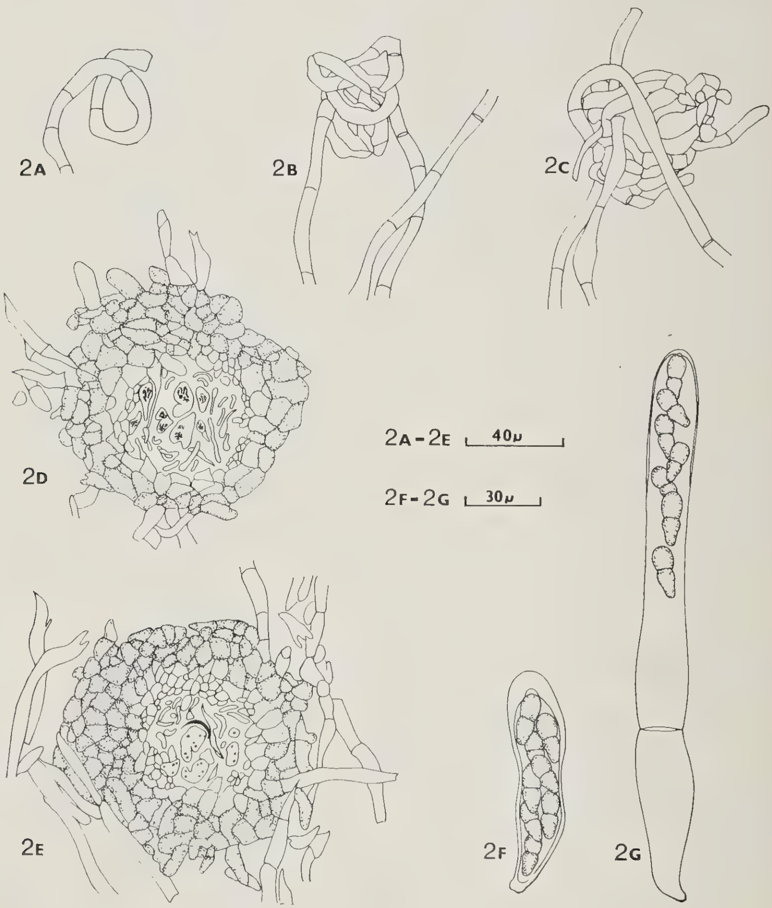
Fig. 1A.
Infected plants of *Erica nemorosa* showing the hypertrophied, black areas on the stems.
Fig. 1B.
Transverse section of infected part of the stem passing through ascocarps and tufts of erect hyphae.
Fig. 1C.
Tufts of erect hyphae with ascocarp initial at the tips.
Fig. 1D.
Vertical section through very young ascocarp. Ascocarp composed of compacted pseudoparenchyma.
Fig. 1E.
Pseudoparaphyses from mature ascocarp (squash preparation), composed of distinctly branched hyphae of uninucleate cells.
Fig. 1F.
Vertical section of ascocarp. Pseudoparaphyses traverse the locule from top to bottom and darker staining ascogenous hyphae grow up between these pseudoparaphyses.
Fig. 1G.
Ascogenous cells concentrated toward the base of the locule with ascal initials growing up between the pseudoparaphyses.
Fig. 1H.
Mature ascocarp with persistent pseudoparaphyses. Asci originate from the base of the locule. (Ascal walls do not show up in the photomicrograph).

twining fungal material. On the stem surfaces, prominent cushions of a cellular construction, brown in colour, are present and from these arise tufts of erect hyphae (Figs. 1B, C) which, due to the closeness of the cushions, appear to completely clothe the infected parts. Ascocarps are to be found associated with the erect hyphae (Fig. 1C).

With regard to the tissue or tissues to which the hypertrophy of the stem could be attributed, both normal, unparasitised stems were sectioned and



observed for comparison with infected stems. Hyphal growth is most extensive in the cortex of the stem. Pockets of hyphae, consisting of threads or compacted pseudoparenchyma and homologous with the cushions of tissue occurring around the stem periphery, contrast with the surrounding yellow to hyaline tissue. Interconnecting hyphae between adjacent hyphal pockets consist of multicellular threads. Such threads, made up of short, uninucleate cells, extensively traverse the primary and secondary phloem as well as most of the secondary xylem. A point of note is the fact that the hyphae are entirely intercellular.

Although cortical tissues and phloem in the infected areas are far wider than those in the uninfected zones, hypertrophy is essentially the result of an excessive production of secondary xylem. In a section through a stem which showed hypertrophy over half its circumference, with the other half uninfected, the secondary xylem was almost double the width of that in the uninfected area. The fungal strands passing through the secondary xylem are continuous and are either separate from the parenchymatous rays or else intermingled with the ray cells. Of comparatively infrequent occurrence are the presence of vertically interconnecting strands from one radial hyphal "ray" to an adjacent one. Transverse interconnecting strands in the secondary tissues have not been seen.

Ascigerous Locule

De Bary (1887) designated the term "symphogenous" to the type of pycnidial development where young hyphal branches interwove to give rise to a compact knot of tissue, this ultimately forming the fruiting body. Such a term might equally be used to describe the initial stages in the development of the ascocarp encountered in this fungus. The erect hyphae clothing the surface of the stem in the infected area do not normally branch. However, some form short loops (Fig. 2A). It appears as if there may be some mechanism governing the formation of ascocarps for it has been observed that only the contiguous hyphae

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Figs. 2A–2C.
Stages from the looping of-, to the anastomosing of the superficial hyphae of the fungus in the formation of an ascocarp.

Fig. 2D.
Transverse section of young ascocarp showing ascogonia surrounded by pseudoparaphyses.

Fig. 2E.
Vertical section of young ascocarp. Centrum composed of multinucleate, lobed ascogonia. Pseudoparaphyses, which have originated above the ascogonia, grow downwards.

Fig. 2F.
Unextended ascus showing the thick wall and containing eight bicellular ascospores.

Fig. 2G.
Ascus after extension with single collar of the ectoascus. Ascospores have moved up toward the apex.

contribute to the formation of any specific fruiting body and that the looping of the hyphae only occur among closely applied strands. Eventually, these hyphae mass and intertwine and form a knot of compacted tissue (Figs. 2B, 2C) which, in the early stages, show a pseudoparenchymatous internal structure (Fig. 1D). In very young stages, these knots are raised well above the surface of the stem (Fig. 1C). This observation was made previously by Doidge (1941) whom, it appears, did not connect the early stages of their development with the looping and anastomosing of the erect hyphae. These ascocarps are gradually drawn downward toward the surface of the host stem and a range of intermediate stages between the very young ascocarp to the mature ones is present at any one time. In the case of the mature ascocarps, these are closely applied to the cushions of pseudoparenchyma mentioned previously (Fig. 1B). Even in this latter state, very short, intertwined hyphae supporting the ascocarps are still evident. Size increase of the ascocarps are the result of the more proximal hyphae anastomosing with the initial mass and also the division and differentiation of the pseudoparenchymatous cells making up the young ascocarp.

Initially, no fusion of the contributing hyphae takes place as seen in a section of a very young fruiting body measuring some 40μ at its largest diameter. In an older ascocarp, 65μ—70μ in diameter, the early stages in differentiation are detectable with the tissue in the centre being decidedly pseudoparenchymatous and consisting of closely compacted, polygonally shaped cells (Fig. 1D). Cell walls of the latter also tend to be lightly staining relative to the darker walls of the outermost cells of the ascocarp. This central tissue of thin-walled cells constitutes the early development of the centrum.

Within the central pseudoparenchyma, changes in structure soon become apparent. From some of the cells, hypha-like outgrowths are produced which, by their elongation, disrupt the neat, contiguous arrangement of cells seen in the previous stage. Concomitant with this development, a number of cells, centrally placed, can be distinguished from the others. These are conspicuous by their prominent nuclei composed of clearly defined chromosomes and nucleoli (Fig. 2D). These are the reproductive initials and are lobed but the compactness of the constituent cells did not allow for distinguishing between a separate ascogonium and antheridium. Consequently, the structures are considered to constitute one or more lobed ascogonia. The surrounding thread-like outgrowths are now more distinct and can be seen to arise from some of the pseudoparenchymatous cells. These are the initials of the pseudoparaphyses (sensu Luttrell, 1965) and they already show septation into component cells. In the vertical section of the ascocarp (Fig. 2E), the outgrowths can be seen to arise from the uppermost cells of the centrum and are most prominent in the region immediately above the ascogonia. The nuclear state of the latter are better defined and their multinucleate condition clearly apparent. Some of the nuclei are

paired, suggesting a dikaryotic phase. The details of plasmogamy and karyogamy have not been elucidated.

In its further development, the ascogonium gives rise to a number of branches, the ascogenous hyphae, which extend up among the vertically orientated pseudoparaphyses (Fig. 1F). The ascogonial branches are distinctly multinucleate with dikaryons apparent here and there. The structurally distinct pseudoparaphyses consist of almost parallel-running strands of cells which traverse the locule from top to bottom, are freely branched (Fig. 1E) and extend from the pseudoparenchyma at the top of the locule and through the ascogenous hyphae to the opposite side. These pseudoparaphyses remain evident throughout the further stages of centrum development. The suggestion by some authors (Cavara & Mollica, 1907 and Arnold, 1928) that the elongation of the pseudoparaphyses is instrumental in the size increase of the fruiting structure has not been ascertained in this study. Nevertheless, it is significant that the growth in length of the pseudoparaphyses does keep pace with the general growth of the ascocarp.

As a result of the rapid elongation of the pseudoparaphyses, the ascogonial complex becomes confined to the lower half or base of the centrum (Fig. 1G) with young asci, each conspicuous by a large fusion nucleus, growing upward amongst the pseudoparaphyses. The asci line the whole base of the locule with a tendency to be more concentrated toward the periphery. Finally, in more mature ascocarps filled with well-developed asci containing ascospores (Fig. 1H), the pseudoparaphyses are still clearly evident with the asci positioned between the strands.

In dry conditions, the globose ascocarps are flattened in the ostiolar area. The apical cells of the outer, dark, thick-walled layers of each of the ascocarps gradually disintegrate to form a pore of irregular outline. The thin-walled pseudoparenchyma and pseudoparaphyses remain as a continuous layer beneath the pore even when the opening has been formed. On wetting, the ascocarp absorbs water rapidly and swells up.

From the ascogenous hyphae, asci arise by typical crozier formation. Asci are clavate (Fig. 2F) and bitunicate and contain eight spores each of which is unequally bicellular, up to 16μ in length and 5μ—6μ in width, slightly constricted at the septum and pluriguttulate. Observations of the bitunicate effect were made on a clump of asci either squashed or dissected out of locules. After extension, the ascus exceeded the length of the original by as much as two and a half times (Fig. 2G). Often, extension was abnormal in that the ectoascus was inclined to split in two or more places with the result that a number of collars or constricting rings were evident. Such a result has also been observed by Luttrell (1951) in *Dothidea collecta* and is considered an atypical condition resulting

from extension in water. In normal extension, only a single collar or ectoascal wall remains.

On spore ejection, the spores are arranged in a single file in the upper half of the ascus and are shot out in quick succession. The orientation of each of the spores is also a consistent feature in that the shorter, blunter hemicell always points toward the apex. After all the spores have been shot out, the ascus contracts, revealing a thick endoascal wall with the ectoascal wall still apparent.

Discussion

The ascocarp in its youngest form is a mass of interwoven hyphae. These hyphae eventually coalesce and give rise to a pseudoparenchymatous structure which is divided into an outer layer of dark, thick-walled cells and a central zone of thin-walled cells. One of these centrally placed cells becomes differentiated into the ascogonium. The latter has thus arisen in a pre-formed stroma and the ascocarp is essentially an ascostroma. This fact, correlated with the bitunicate ascus, would place *Antennularia engleriana* in the subclass Loculoascomycetes (Luttrell, 1955).

The term, psuedoparaphyses, used here to describe the hypha-like structures which traverse the centrum from top to bottom is as defined by Luttrell (1965). As far as can be deduced from the sectioned material, these structures originate as outgrowths from the stromal cells especially those above the ascogonial complex. With subsequent downward growth, which may be mainly intercalary, they take on an almost vertical orientation and are attached at both ends. Their distinct, thread-like, branched and cellular make-up has been emphasized. According to Singer and Gamundi (1963) the term 'paraphysoid hyphae' has been ascribed to threads which are originally attached to the top of the ascocarp and which grow down but remain free from the bottom, and 'paraphysoid threads' for hyphal outgrowths attached at both top and bottom of the ascocarp from the beginning of development. Ontogenetic details of these two types do not strictly apply to the structures encountered in this fungus. Gäumann (1926) applied the term 'pseudoparaphysis' to the thread-like structures in the Loculoascomycetes, noting 'paraphysoid' (sensu Petrak, 1923) as a synonym. The objection against the use of 'pseudoparaphysis' is twofold. Firstly, it has been applied to an hymenial element in certain Basidiomycetes. Secondly, Petrak (1923) employed 'pseudoparaphysis' to describe hypha-like outgrowths which were free at the tips but these are better known as true paraphyses. The use of 'paraphysoid' has been avoided due to its application to both pseudoparaphysis and interthecial tissue. Further emphasis on the use of 'pseudoparaphysis' has been made by Luttrell (1965) who stresses these are the only distinctive structures in the Loculoascomycetes for which a special term is

warranted. The mode of origin and the development of the structures as found in this fungus corresponds with Luttrell's description and the terms 'pseudo-paraphysis' has been employed here.

The pseudoparaphysate centrum and the perithecium-like ascostroma places *A. engleriana* in the order Pleosporales (sensu Luttrell, 1955). Müller and von Arx (1950, 1962) have retained the order Pseudosphaeriales, established by Theissen and Sydow (1918), in which are included forms with uniloculate, perithecium-like ascostromata. The order Pleosporales has been used here instead of Pseudosphaeriales because of the indiscriminate inclusion in the latter of forms in which the centra contain either pseudoparaphyses or interthecial tissue. These structures, as indicated by developmental evidence, are not homologous.

It must be reiterated that the use of the generic name, *Antennularia* in preference to *Dimerosporiopsis* is tentatively agreed upon until other forms included in the former genus have been investigated. In fact, until investigations are carried out over a broader range among species grouped in the Pleosporales (of Luttrell) and the Pseudosphaeriales (of Müller and von Arx), can more definite criteria for subdivisions into various families be proposed.

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DEVELOPMENTAL MORPHOLOGY OF A NEW LOCULOASCOMYCETE ON *EUPHORBIA*.

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Abstract

A new genus in the Loculoascomycetes is described. Infection is initiated by germ tubes from ascospores penetrating the stomata on the stems of the host. Stromata eventually appear above the stomata and from these, plates of prosenchyma form parallel with the stem surface. More stromata arise from these plates of cells. Centrum development of the ascocarp is of the Dothidea type, with the asci growing up into a space which results from the disintegration of pseudoparenchyma. An unusual feature in the development of the various structures is the prevalence of intracellular cleavage of multinucleate cells to form uninucleate ones.

Uittreksel

DIE ONTWIKKELINGS MORFOLOGIE VAN 'N NUWE LOCULOASCOMYCETE OP *EUPHORBIA*.

'n Nuwe genus in die Loculoascomycetes word beskrywe. Besmetting word deur kiembuise van askospore, wat die stomatas op die stamme van die gasheer, binne dring aan die gang gesit. Stromas verskyn uiteindelik bo die stomatas en hieruit, ontwikkel plate van prosenchiem wat parallel met die oppervlak van die stam groei. Verdere stromas ontwikkel dan uit hierdie plate van selle. Die ontwikkeling van die sentrum van die askokarp geskied volgens die Dothidea tipe: die askospore groei in 'n ruimte wat as gevolg van die afbreek van die dieper weefsel ontstaan. 'n Buitengewone kenmerk in die ontwikkeling van die verskillende strukture is die frekwente intrasellulêre verdeling van veelkernige selle om eenkernige selle te vorm.

Introduction

This fungus described here is parasitic on the stems of *Euphorbia bothae* Lotsy & Godd. Uniloculate ascostromata, interspersed with microconidial locules, form superficially, in concentric rings, upon the epidermis (figs. 1A, B).

Communication with the National Herbarium, Pretoria, (Marasas, 1969—Personal communication) has revealed that the only Ascomycete recorded on *E. bothae* is one with a pulvinate stroma with ascigerous locules arranged in a peripheral layer on this stroma and has been labelled as '*Dothidea* sp. indet'. These stromal characteristics do not compare with this fungus being studied.

In the keys of Clements and Shear (1957), this fungus cannot be accommodated easily into any of the genera listed in the phaeodidymous Sphaeriaceae or Dothideaceae. Employing the keys of Müller and von Arx (1962) this fungus is best placed in the Pseudosphaeriales and in the Dimeriaceae or possibly,

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the Mycosphaerellaceae. However, in the genera in both families closest to this fungus in description, these are invariably featured as having 'paraphysoids' among the asci. As interascicular structures are lacking in this fungus, it cannot be accommodated in either family.

Since, after an examination of modern literature, this species could not be placed in a suitable genus, it was decided to describe it as a new genus and species.

SCUTELLOIDEA TIM, gen. nov., (Dothideaceae, sensu Luttrell, 1955).

Stromata superficialia, unilocularia, atrobrunnea sive nigra. Stromata acervis solutaris cellarum coperta. Loculi in stromatibus formati quae et in et super stomatibus crescent vel gignunt ex incremento laminarum prosenchymatis quae ipsae ex stromatibus evolvunt et paralleles superficiei hospitis oriuntur. Asci cylindrici, octospori, bitunicati, aparaphysati. Sporae brunneae, bicellulares.

Type species: *S. concentrica* Tim.

Stromata superficial, uniloculate, brown to black in colour. Stromata covered in detachable clumps of cells. Locules formed in the stromata which in turn arise in and above stomata or as a result of the proliferation of the plates of prosenchyma which arise from the stromata and grow parallel with the surface of the host. Asci cylindrical, eight spored, bitunicate, aparaphysate. Ascospores brown, bicellular.

Etymology: L. scutellum=shield.
Gk. eidos=form.

Scutelloidea concentrica Tim, sp. nov.

Stromata caulicola, superficialia, uniloculata, saepe confluentia, 88—113=110—175μ, ex medio evoluta et plus minusve concentrice disposita. Asci octospori, cylindrici, 75—88$\times$20—25μ, bitunicati, aparaphysati. Sporae medio vel paullo supra medium septatae, leniter constrictae, 25—30$\times$6—8μ.

Type: South Africa, Cape—3326A (Grahamstown): Hell's Poort, *Tim* 198 (PRE, holo.; K, iso.).

Stromata caulicolous, superficial, uniloculate, may be confluent, 88—113$\times$110—175μ, developing centrifugally and arranged in concentric rings. Asci eight spored, cylindrical, 75—88$\times$20—25μ, bitunicate, aparaphysate. Spores two celled, medially septate or cells subequal, very slightly constricted, 25—30$\times$6—8μ.

Etymology: L. cum=together; centrum=centre.
Habitat: Stems of *Euphorbia bothae* Lotsy and Godd.

Materials and Methods

Infected stems of *Euphorbia bothae* were collected on a farm in Hell's Poort, Grahamstown during the period July to January, 1965—1966, 1966—1967. The earliest stages in development were usually evident during August whilst the mature stages were present throughout the year.

Slices of tissue containing stromata $\frac{1}{8}''$ (or 3 mm) in thickness, were removed and the excess latex wiped away. It was important that the latex did not cover the stromata as this would have trapped particles of grit among the fruiting bodies which would interfere with the process of sectioning. Small squares of infected tissue were fixed in form-acetic-alcohol, carried through a butyl alcohol series and imbedded in 55—60° wax. Sections were cut at 6—10μ and stained in Heidenhain's haematoxylin with a counterstain of Orange G (Johansen, 1940). Temporary preparations were mounted in cotton blue in lactophenol.

For the examination of the details of spore germination on the stem, infected areas were coated with two layers of clear nail varnish and left to dry for 12 hours. The strips were carefully removed after freeing the edges with a scalpel and mounted in cotton blue in lactophenol.

Host-Parasite Relations

Ascospores are produced in abundance from the numerous ascocarps which cover large areas of the stem. However, very few of these spores actually germinate on the stem, and of those which do, only a small proportion gain entrance into the host. To elucidate some of the factors governing spore germination, the following was carried out: Segments of infected stem were positioned about 5 cm above clean stems selected from the tops of the plants. These were left overnight in a moist atmosphere to induce spore ejection onto the uninfected stems. After this treatment, the stems were placed outdoors in a protected position and at three day intervals, a nail varnish strip was made of the newly infected part.

The number of spores germinating with time did not increase significantly. Spores which germinated near stomata exhibited a more precocious development than those which germinated away from stomata. The same was found for spores germinating near a crack in the cuticle. It was thus concluded that the unusually thick cuticle afforded an effective barrier against invasion by this fungus. The fact that germ tubes ramified between cracks in the cuticle seemed to indicate that it was unlikely that invasion through stomata was due to stimulation by a specific factor or set of factors associated with stomata as spore germination occurred near to as well as away from stomata. When germ tubes were produced some distance from a stoma, they showed randomised

growth and were light in colour. Those tubes near a stoma were darker in colour, penetrated into the opening directly and produced a small knot of dark cells above the guard cell (figs. 1C, D). From such a knot, a hypha would grow inward between the guard cells (fig. 1D) and invade the substomatal cavity, filling this with hyphae. Invasion of the host takes place from this part and hyphae penetrate between the cells, entering the deeper tissues of the host. At all times, the hyphae, which are composed of multinucleate cells, remain intercellular, do not have haustoria and do not penetrate very deeply into the tissue; the infected area remains relatively superficial and there is no attendant hypertrophy evident.

Subsequent to the hyphal invasion of the internal tissues, dark aggregations of hyphal cells concentrate near a number of stomata in close proximity to

each other. These fungal cells increase and displace the guard cells in the process (fig. 1E) and are the initials of the fruiting bodies. In other words, the fungus gains access into the host by way of the only natural openings, the stomata. After invasion of the tissue, these stomata serve as the exits for the fungus and it is on the surface of the stem that further development takes place (fig. 1F).

Each stromal initial proliferates, forming a cone of pseudoparenchyma (fig. 1E). From this cone, the outermost cells in localised areas divide, forming paradermal plates of tissue mostly one cell in thickness and these lie in parallel sheets (figs. 1E, F) raised a short distance from the surface of the stem. The appearance of a young stroma in vertical section is very much that of a pagoda.

Proliferation of the hyphae of the plates occurs by means of intracellular cleavage. In each cell, the protoplasm is seen to divide into a number of separate portions (fig. 1G). Each portion may again divide so resulting in a bulging-out of the wall of the parent cell. In this way, the prosenchyma becomes propagated in all directions. The plates retain their hyphal construction for most part and coalesce with adjacent plates. At any point between stomata, the cells of these plates may proliferate and form a knot of pseudoparenchyma which also gives rise to a fruiting body and hence the number of fruiting bodies per unit area becomes considerable (fig. 1F). In the formation of a stroma, a few of the hyphae of the plates grow upward and undergo a series of intracellular cleavages to form a knot of cells. The process continues, with more cells being added to the developing stroma. Even when the fruiting structures, whether ascocarps or

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Fig. 1A.
Infected portion of the stem of *Euphorbia bothae*, with compact masses of uniloculate ascostromata and microconidial locules grouped on the stem surface.

Fig. 1B.
A single infection showing the concentric arrangement of bands of fruiting bodies.

Fig. 1C.
Germinated ascospore near a stoma. A knot of hyphae is produced from the germ tube just above the stoma.

Fig. 1D.
Hypha growing out from the knot of hyphae above a stoma and penetrating between the guard cells of the host.

Fig. 1E.
Cone of pseudoparenchyma of a stromal initial formed in the immediate region of a stoma and displacing the guard cells. Paradermal plates of tissue are produced from the stromal mass.

Fig. 1F.
Vertical section through an infection showing the superficial, uniloculate ascostromata formed from the stromal proliferations through stomata or from stromata formed from the paradermal plates.

Fig. 1G.
Cleaved protoplasts of cells of the paradermal plates.

Fig. 1H.
Vertical section through a multiloculate microconidial locule. Microconidia escape throu a number of openings.

microconidial locules, are mature the surface cells continue this protoplasmic cleavage (fig. 2A) so resulting in the surface being covered with these muriform aggregations of cells. However, they differ from the cells forming the parallel plates in that these cells which have undergone protoplasmic cleavage do not go on dividing indefinitely to form plates of tissue but remain as loose clumps of cells which add to the bulk of the fruiting bodies and are easily brushed off from the surface. Their role, if any, in the biology of the fungus is unknown.

The fruiting bodies, to begin with, form a dense patch, occupying a circular area up to 3 mm in diameter. Eventually, the infection spreads, still in a circular manner, with a relatively clear zone remaining between the original infection and the next band. This process may continue till the area of fruiting bodies is some 2 cm in diameter, consisting of from four to six separate bands (fig. 1B). The concentric banding itself may be due to seasonal effects. From previous observations, only ascospores germinating near stomata produce an infection. The chance of a number of stomata in close proximity being infected is highly likely even under natural conditions, as the volume of spores produced from such abundant stromata must, logically, be tremendous. What remains puzzling is why a considerable area of stem is not covered by fruiting bodies from the start and why coalescent circles of infection are relatively rare. Old parts of the stems do show a considerable intergrading of circles of the fungus but this is the result of the original rings increasing in number with time. Perhaps there is some sort of inhibitory reaction whereby the first spore to gain access into the plant sets up a barrier which inhibits the further development of other germinated spores in the immediate vicinity.

Microconidial locules

The first fruiting bodies to be produced during the early phases of infection are the microconidial locules. In the cone-shaped mass of pseudoparenchyma formed above each stoma, a lighter staining portion in the centre becomes obvious. On closer examination when the structure is of a reasonable size, fertile portions producing microconidia can be seen to arise in a number of parts within the central, lighter staining part. As each of the parts producing microconidia develops at a different rate, the structure appears to be multiloculate. Because of its amorphous shape (fig. 1H) a microconidial locule is clearly distinguishable from an ascigerous locule and at maturity measures $50—110 \times 65—135\mu$. The same procedure in locule formation takes place in the stromata developed on the hyphal plates between stomata.

The formation of microconidia takes place centrifugally. Microtome sections did not provide conclusive information as to the origin of the microconidial mother cells; squash preparations of young stromata proved far more satisfactory here.

Initially, in each locule, the pseudoparenchyma takes on a loose appearance and each cell can be seen to have dense protoplasm with a number of nuclei. Each cell destined to form microconidial mother cells becomes somewhat elongated and points toward the centre of the locule. The protoplast undergoes cleavate so forming a row of segments (fig. 3A). Cell walls eventually form and the whole structure consists of a row of cells, each with a single nucleus. The squash preparations showed most of the developmental stages. Individual portions in each of the cleaved cells stained up with the cotton blue whilst the wall of the original cell investing the portions remained hyaline.

After wall formation, each portion becomes a mother cell. Microconidia are first produced from the terminal cell. The tip of this cell becomes drawn out to form a symmetrically placed sterigma from which a bacilliform microconidium is cut off. The microconidia are uninucleate, 1,8—2,5 $\times$ 0,7—0,9μ, and even when still attached to the mother cell, the latter is seen to contain a prominent nucleus. It can only be presumed that each mother cell is capable of giving rise to more than one microconidium. Cells lower down the series may also produce sterigmata. It seems logical to conclude that after a number of microconidia have been formed, each mother cell disintegrates, its role being continued by other cells further down the series. Cells deeper in the pseudoparenchyma lining the locule assume similar functions after their protoplasts cleave. This would account for the progressive enlargement of the locule with the concomitant growth in size of the stroma.

The microconidia fill the locule and ooze out through a number of irregular openings which break through the outer layers of the stroma. The actual role of these microconidia in this fungus is presumed to be spermatial. Their small size and abundant production are features similar to structures in other fungi where their spermatial function has been ascertained.

Ascigerous Locules

Ascostromata are initiated in the same way as the microconidial locules. Mounds of pseudoparenchyma arise either above the stomata or form as a result of the proliferation of the prosenchyma lining the surface of the host. Whilst stromata destined to become microconidial locules show the presence of microconidia at a very early age in the lighter staining central mass of cells, ascostromal masses appear more compact to begin with. The central mass soon loses its compactness and the cells appear almost separated from one another (fig. 2A). Among these cells, a loose, partially coiled, multinucleate structure arises with a projection reaching up toward the apex. In a few cases, these projections appeared to penetrate the outer, dark layers of the stroma and to reach the outside (fig. 3B). This structure is possibly the ascogonium with trichogyne.

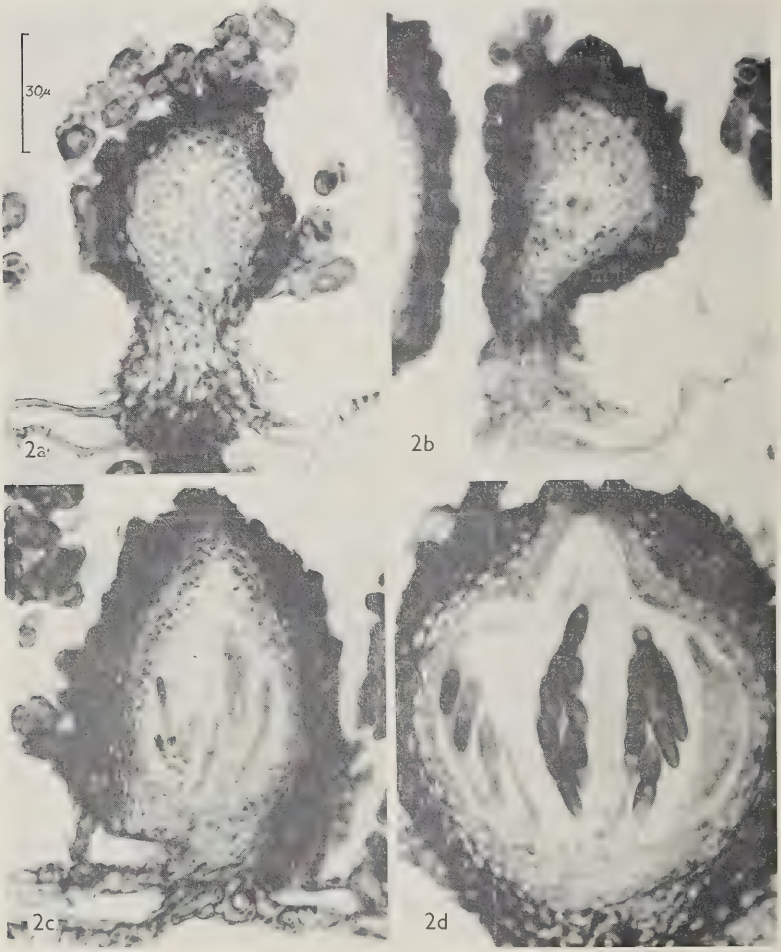

Fig. 2A.
Vertical section through a young ascostroma showing a separation of the internal pseudoparenchyma cells. Note the masses of cleaved protoplasts, still invested by the original cell walls, clustered around the outside of the fruiting body.

Fig. 2B.
Lobed ascogonium, with a number of pairs of nuclei, situated in a space which has resulted from the distintegration of the centrum pseudoparenchyma. Note the inwardly pointing rows of cells originating from the pseudoparenchyma lining the dark outer layers of the ascostroma.

Fig. 2C.
Branched ascogenous system from which asci arise. Each ascus has a fusion nucleus.

Fig. 2D.
Mature ascostroma with prominent ostiolar area at the top.

The area around the ascogonium becomes progressively more open and soon, is surrounded by a space with the cells lining the inner part of the ascocarp pointing inwards (fig. 2B). These latter cells are elongate and consist of a number of fragmented portions of the protoplast of single cells with each fragment having its own nucleus. Cell walls eventually delimit these portions in a linear series in the same way as was noted for the microconidial mother cells. Due to their limited growth these chains of cells cannot be considered homologous with pseudoparaphyses (sensu Luttrell, 1965). The formation of the space around the ascogonium comes about as a result of the breakdown of the centrum cells. Remains of these cells in the form of extremely fine cell walls, devoid of contents, can be detected around the ascogonium. These often appear as fine threads connecting the ascogonium to the surrounding stromal layers.

Figure 2B shows a lobed ascogonium with a number of pairs of nuclei, indicating that plasmogamy has already occurred. Cell walls are not apparent and the ascogonium is still multinucleate. Cell walls eventually form and the ascogonial complex is then made up of a number of cells in a chain-like series, somewhat reminiscent of the cells from which the microconidia arise. Short lateral branches grow out from some of the individual cells and the binucleate condition becomes perpetuated into these arms. These constitute the ascogenous hyphae and radiate out from a complex of cells toward the base of the locule. Such a complex of ascogenous cell from which asci arise, was also recorded in *Dothidea collecta* (Luttrell, 1951a).

In each of these short ascogenous hyphae, the two nuclei fuse directly, giving rise to the fusion nucleus in the ascus initial. Croziers are not formed. This ascus initial becomes much enlarged and vacuolate and the single fusion nucleus stands out prominently (fig. 2C). As ascus development progresses, the whole locule enlarges and the clear area around the ascogenous system becomes wider allowing for the ingrowth of asci to carry on without hindrance from extraneous tissue. At the apex, a beak develops and is lined with rows of cells similar to those which line the rest of the locule. These, however, are longer and persistent and remain as the periphyses whereas the others in the main body of the locule soon lose their identity, possibly as a result of the crowding by asci (fig. 2D). A pore finally breaks through the dark layers of the ascocarp. The latter, at maturity, is perithecium-like in form and of dimensions $88—113 \times 110—175\mu$. Eight bicellular ascospores are produced in each ascus. The spores are dark in colour, $25—30 \times 6—8\mu$, and are composed of two equal to subequal cells with a waist at the septum. The asci are cylindrical (fig. 3C), $75—88 \times 20—25\mu$, and bitunicate (fig. 3D) and on extension, the endoascus of each ascus in turn reaches through the pore and the spores are shot out in quick succession.

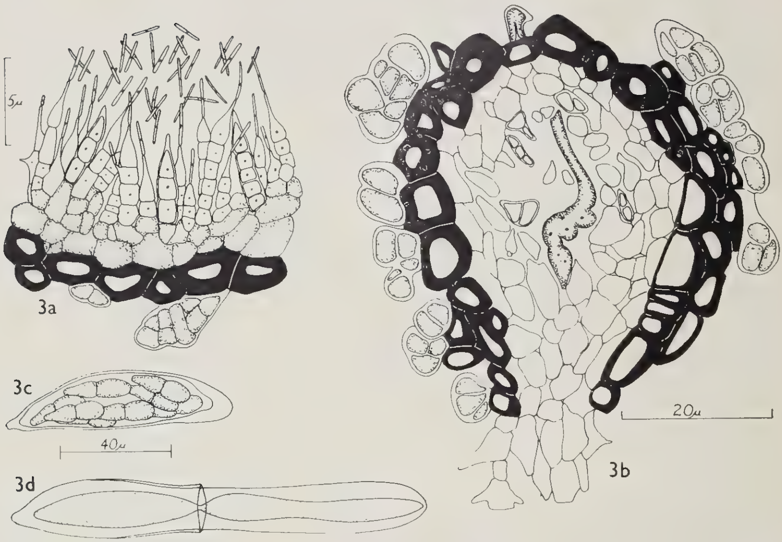

Fig. 3A.
Microconidial mother cells originating as cleaved portions of the protoplasts of cells lining a locule. A sterigma, from which microconidia are produced, is usually formed from each of the portions.

Fig. 3B.
Ascogonium with trichogyne in a young ascostroma.

Fig. 3C.
Unextended ascus with ascospores.

Fig. 3D.
Ascus after extension of endoascal wall through the ectoascal wall. Spores already ejected.

Discussion

The early ascigerous locule consists of a compact mass of pseudoparenchyma composed of thick walled peripheral cells devoid of stainable contents and thin-walled, nucleated cells of the centrum. Within the latter, an ascogonium becomes differentiated and such development would make the fruiting structure an ascostroma. This, together with the presence of the bitunicate ascus would place *Scutelloidea concentrica* in the Loculoascomycetes (Luttrell, 1955).

The fact that this fungus is described in a new genus, the specific definition of the general stroma is important. The initial stromata emerge from the stomatal openings and are positioned superficially on the surface of the host. From these stromata, plate of prosenchyma grow out, invest the surface of the stem and further stromata form as a result of the proliferation of cells of these

plates. These parallel plates would therefore also constitute the stroma. The uniloculate ascostromata would be correctly described as being situated above stomata or on a stromal base arising from plates of prosenchyma which lie parallel with the stem of the host.

Disruption of the centremost cells of the centrum progresses to the point where the asci grow up into a space. Interascicular structures such as paraphyses, pseudoparaphyses, interthecial tissue (sensu Luttrell, 1965) are absent. Such development would conform with the Dothidea type and would place *Scutelloidea* in the Dothideales (Luttrell, 1951b). It would also be conveniently included in the Dothideaceae due to the perithecium—like locule and fasciculate arrangement of asci.

The frequent occurrence of protoplasmic cleavage as a form of cell division in *Scutelloidea concentrica* is a feature shared with *Dothidea collecta* (Luttrell, 1951a). It appears that almost all the cells, to begin with, are multinucleate. As a result of intracellular divisions, the uninucleate condition is brought about in all cells with the exception of the ascogenous hyphae where binucleate cells are delimited.

Acknowledgments

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Grateful thanks to Professor E. S. Twyman for his supervision throughout the course of this work. Thanks are also due to Mr. J. P. Jessop for his helpful criticism and to Dr. B. J. Cholnoky and Prof. B. Dietrich for their checking of the Latin diagnosis.

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Jl S. Afr. Bot. 37 (3): 169–176 (1971)

TAXONOMIC NOTES ON *ERICA*

H. A. Baker

Abstract

In an endeavour to clear up the large number of specimens of *Erica* in the herbaria as yet unclassified in the section *Trigemma*, this section has been subjected to a critical study. Four new species are proposed and described in detail.

Uittreksel

TAKSONOMIESE NOTAS OOR *ERICA*.

In 'n poging om die groot aantal onbenaamde eksemplare van Erica, in die seksie Trigemma wat in die herbaria is, te verduidelik, is hulle blootgestel aan 'n kritiese bestudering. Vier nuwe soorte word voorgestel en volledig beskryf.

Introduction

The recent collection of material belonging to *Erica* section *Trigemma* of the subgenus *Chlamydanthe* led the author to study all the material at present regarded as *incertae* and placed tentatively in that section in the local herbariums, BOL, NBG and SAM. The four new species here described have reduced the incertae in this section to a few pieces of inadequate material.

Those now described are all small, bushy shrublets growing at high altitudes on the mountains East of Paarl to the Swartberg range. Their general appearance as pressed specimens is rather similar superficially but, on close examination many important differences are revealed sufficient, in the author's opinion to merit specific rank.

Unfortunately most of the speciments are of such an age that, even after boiling, it is not possible to ascertain with exactness the shape of the corolla and the effusion of the lobes. The latter appear to be continuous in most cases but it is more likely that they are more or less reflexed as in the live specimens of *E. altevivens* studied.

It is most desirable that, in future, material that cannot be classified at once should have a pencil sketch of the flower and a mounted dissection made while the specimen is still fresh. These, together with full descriptions of the locality and a note as to colour should be placed with the specimens. If these simple requirements were to be fulfilled the labour of future classification would be greatly reduced and the value of the work enhanced.

Erica altevivens H. A. Baker, sp. nov. (Ericaceae—Ericoideae) Trigemma. Fruticulus erectus ramosus, caudice lignoso, ad 30 cm altus. *Rami* ramulis

numerosis, tenuibus, puberuli ubi juniores, demum glabri et cicatricibus foliorum delapsorum notari.

Folia 3—nata, 2—3 mm longa, erectopatentia, imbricata, oblonga ad anguste elliptica, acutata, breviter mucronata, obscure sulcata, glabra, junioria

ciliata. *Flores* terminales, pro parte maxima 3—nati, interdeum 4—nati, saepe cernui, interdum secundi, calycini; pedunculi 3—4 mm longi, saepi curvi, pubigeri; bracteae pro parte maxima subapproximatae sed interdum una vel omnes remotae, 1—3 mm longae, sepaloidae sed parviorae et angustiorae. *Sepala* 2,5 mm longa, angustae ad subulatae ovata, concava, carinata et apicubus carinatis, scariosa, glabra, parce ciliata setis caducis, ejusdem coloris quam corollae. *Corolla* circa 3,5—4 mm longa, subcampanulaticyathiformis vel urceolata, sicca, glabra, alba vel interdum subrosea; lobis 1,2 mm longis, erectis vel recurvis, acutatis. *Filamenta* gracilia, linearia; antherae inclusae, 1 mm longae, subterminales, angustae oblongae, basibus obliquis junctus, ad bases bipartitae, casteneae, cristatae; poro fere pars dimidio lobi; cristae 0,6 mm longae, pendens, latae, decrescens et ad bases acutae, varie dentatae vel laeves. *Ovarium* depresso-globosum, glabrum; stylo incluso; stigmate capitellato.

Erect much branched shrublet from a woody rootstock to 30 cm or so. *Branches* with many delicate branchlets, puberulous when young, later glabrous and marked with the scars from the fallen leaves. *Leaves* 3—nate, 2—3 mm long, erect-spreading, imbricate, oblong to elliptic, acute, shortly mucornate, obscurely sulcate, glabrous, minutely ciliolate when young. *Flowers* terminal, mostly 3—nate but, occasionally, 4—nate, often cernuous, sometimes secund, calycine; peduncles 3—4 mm long, often curved, pubigerous; bracts mostly subapproximate but variable and sometimes one or all remote, 1—3 mm long sepal-like but smaller and narrower. *Sepals* 2,5—3 mm long, narrow to broadish ovate, concave, keeled and keel-tipped, scarious, glabrous, ciliate with variable, caducous setae, coloured, *Corolla* 3,5—4 mm long, urceolate to subcampanulate-cyathiform, dry, glabrous, white or occasionally pale pink; lobes slightly spreading, acute, about $\frac{1}{3}$ the length of the tube. *Filaments* linear, slender; anthers included, 1 mm long, subterminal, narrow-oblong, deeply bipartite, oblique at the base where the cells are united, chestnut-brown, crested; pore about half the length of the cell; crests 0,6 mm long, pendulous, fixed near the base of the lobes, broad but narrowing to a tooth at the apex, variously toothed. *Ovary* globose to depressed-globose, glabrous; style included; stigma capitellate.

ERRATUM

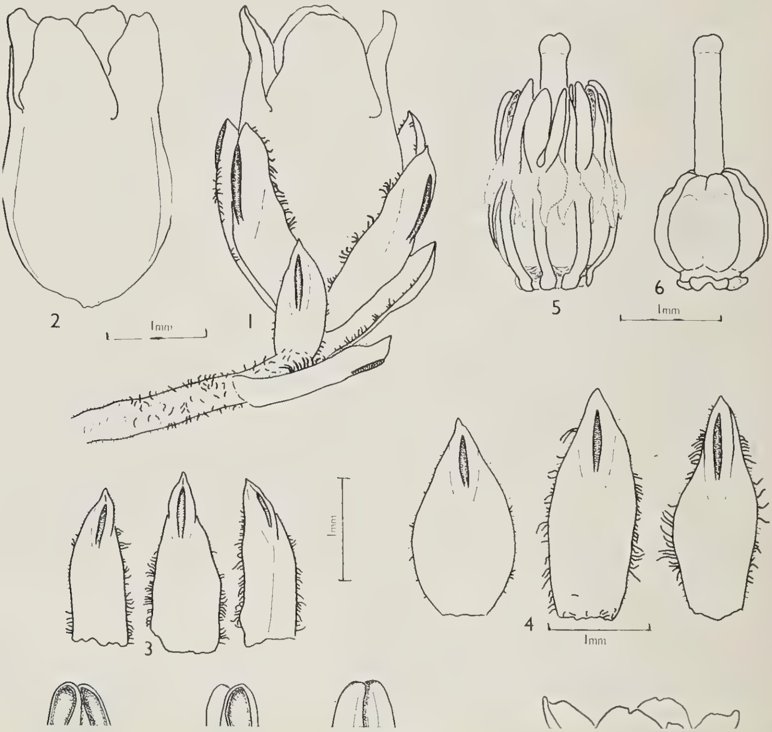
Journal of South African Botany, Vol. 36 Part 1: 13-52 (1970).
"Euphorbia species from the Flora Zambesiaca Area IX"

In the key on page 15 the "Inflorescence" clue leading to *Euphorbia grandicornis* should read:

Inflorescence with 1-3 cymes regularly transversely arranged, with the central male cyathium usually *persistent*.

numerosis, tenuibus, puberuli ubi juniores, demum glabri et cicatricibus foliorum delapsorum notari.

Folia 3—nata, 2—3 mm longa, erectopatentia, imbricata, oblonga ad anguste elliptica, acutata, breviter mucronata, obscure sulcata, glabra, junioria



ciliata. *Flores* terminales, pro parte maxima 3—nati, interdeum 4—nati, saepe cernui, interdum secundi, calycini; pedunculi 3—4 mm longi, saepi curvi, pubigeri; bracteae pro parte maxima subapproximatae sed interdum una vel omnes remotae, 1—3 mm longae, sepaloidae sed parviorae et angustiorae. *Sepala* 2,5 mm longa, angustae ad subulatae ovata, concava, carinata et apicubus carinatis, scariosa, glabra, parce ciliata setis caducis, ejusdem coloris quam corollae. *Corolla* circa 3,5—4 mm longa, subcampanulaticyathiformis vel urceolata, sicca, glabra, alba vel interdum subrosea; lobis 1,2 mm longis, erectis vel recurvis, acutatis. *Filamenta* gracilia, linearia; antherae inclusae, 1 mm longae, subterminales, angustae oblongae, basibus obliquis junctus, ad bases bipartitae, casteneae, cristatae; poro fere pars dimidio lobi; cristae 0,6 mm longae, pendens, latae, decrescens et ad bases acutae, varie dentatae vel laeves. *Ovarium* depresso-globosum, glabrum; stylo incluso; stigmate capitellato.

Erect much branched shrublet from a woody rootstock to 30 cm or so. *Branches* with many delicate branchlets, puberulous when young, later glabrous and marked with the scars from the fallen leaves. *Leaves* 3—nate, 2—3 mm long, erect-spreading, imbricate, oblong to elliptic, acute, shortly mucornate, obscurely sulcate, glabrous, minutely ciliolate when young. *Flowers* terminal, mostly 3—nate but, occasionally, 4—nate, often cernuous, sometimes secund, calycine; peduncles 3—4 mm long, often curved, pubigerous; bracts mostly subapproximate but variable and sometimes one or all remote, 1—3 mm long sepal-like but smaller and narrower. *Sepals* 2,5—3 mm long, narrow to broadish ovate, concave, keeled and keel-tipped, scarious, glabrous, ciliate with variable, caducous setae, coloured, *Corolla* 3,5—4 mm long, urceolate to subcampanulate-cyathiform, dry, glabrous, white or occasionally pale pink; lobes slightly spreading, acute, about $\frac{1}{3}$ the length of the tube. *Filaments* linear, slender; anthers included, 1 mm long, subterminal, narrow-oblong, deeply bipartite, oblique at the base where the cells are united, chestnut-brown, crested; pore about half the length of the cell; crests 0,6 mm long, pendulous, fixed near the base of the lobes, broad but narrowing to a tooth at the apex, variously toothed. *Ovary* globose to depressed-globose, glabrous; style included; stigma capitellate. Flowering season, midsummer.

Distribution. CAPE—3319 (Worcester): Rocky places from circa 1220 m to the mountain summits; Winterberg (—CC), Jan. 1960, *Esterhuysen 9628* (holotype in BOL, isotypes NBG, PRE, STE.); Wildepaardeberg (—CD), Jan. 1925, *Stokoe 1056* (BOL, NBG); Wemmershoek Peak (—CC), Jan. 1951, *Esterhuysen 1253* (BOL, NBG); Slanghoek Pile (—CC), Jan. 1940, *Esterhuysen 1739* (BOL); Witteberg Rocks (—CA), Feb. 1943, *Esterhuysen 8671* (BOL);

Fig. 1

Erica altevivens H. A. Baker

1. Flower; 2. Corolla; 3. Bracts; 4. Sepals; 5. Androecium and Gynoecium; 6. Gynoecium; 7. Anther, front, side and back view—all from Esterhuysen 9628 (Bol); 8. Corolla, from Bol 30676. del. E. G. H. Oliver.

(*a*) (*b*)

FIG. 2. *Photo: H. A. Baker*

Erica altevivens, sprigs from different plants.
(*a*) approx. $\frac{1}{3}$ natural size, (*b*) approx. natural size of Bol. 30676.

Stettynsberg (—CC & CD) c. 1525 m, Jan. 1970, *W. P. U. Jackson s.n.* (BOL *30676*, NBG, PRE, STE); du Toit's Peak (—CC), Jan. 1943, *Esterhuysen 8596* (BOL); Limietberg (—CA), Mar. 1940, *Esterhuysen 1603* (BOL); Wellington Sneeuwkop (—CA), Feb. 1943, *Esterhuysen 8639* (BOL); Bayley's Peak (—CA), Feb. 1942, *Stokoe 8340* (BOL); Seven Sisters Mt. at the head of Groen Kloof (—AC). Jan. 1955, *Esterhuysen 18313* (BOL, NBG), 3419 (Caledon); Genadendal Mts. (—AB & BA) Feb. 1936, *Stokoe 6927* (BOL).

E. altevivens has frequently been collected west of Worcester and is a well established species. It is here placed in section *Trigemma* rather than *Euryloma* because the corolla, though variable, is never wide-mouthed as in the latter. In the most recent collection, not selected as the type, the author has been able to study the plant in the wild state. In this case the corolla, typically urceolate, differs from many of the other collections, including the type, in which it is subcampanulate-cyathiform, a rather clumsy term used by Guthrie & Bolus in *Flora Capensis* 4: (1909) for this shape.

In structure this species is nearest to *E. acuta* Andr. but there are many differences in detail and dimension. The rather peculiar anthers are, however, similar.

Possibly through being confined to the upper altitudes of the mountains and thus, in some degree, in isolated colonies, the species is variable in some respects but not sufficiently so to warrant the creation of varieties. The variations noted in examining all the species cited have been included in the description.

The parts of the plant that have hairs as in the description have, intermingled with these white ones, some deeply pigmented, caducous 'hairs' the purpose of which is obscure.

Erica blesbergensis H. A. Baker, sp. nov. (Ericaceae-Ericoideae). Trigemma.

Fruticulus erectus, densus, humilis. *Rami* graciles, ramulis numerosis, ascendens, glabri, cicatricibus foliorum delapsorum notari. *Folia* 3—nata, 1,5—2 mm longa, initio erecta et imbricata demum quam internodka breviora et adpressa, ovales acutata, supra plana, crassa, carinata, obscure sulcata marginibus scariosis et seticiliatis, glabra. *Flores* terminales, 3—nati, calycini, pauci; pedunculi, 2 mm longi, glabri; bracteae medianae, 1 mm longae, sepaloides sed parviorae et angustiorae. *Sepala* c. 2 mm longa, ovata sed variabila, crassa, concava, scariosa, rigidocarinata apicibus sulcatis, glabra, setis caducis ciliata. *Corolla* 2,75—3,0 mm longa, subcampanulatocyathiformis, sicca, glabra, tenuis, alba; lobis continuis vel, ad matutitatem, probabiliter effusis, c. 0,9—1,0 mm longis, obtusis. *Filamenta* ligulata; antherae inclusae, 1 mm longae, laterales, oblongae, bipartitae sed non diffusae, muticae; poro fere pars tertia lobi. *Ovarium* turbinatum vel subglobosum, superne sparse villosum, stylo incluso; stigmate cyathiformi, manifesto, grandi.

Erect, low, dense, twiggy shrub. *Branches* ascending, many, slender, the older leaf-scarred, glabrous. *Leaves* 3—nate, 1,5—2 mm long erect and imbricate at first, later, with the elongation of the branches, shorter than the internodes and adpressed, oval, acute, flat above, thick and keeled, obscurely sulcate, scarious-edged and setose-ciliate, glabrous. *Flowers* terminal, 3—nate, calycine, few; peduncules 2 mm long, glabrous, red; bracts median 1 mm long sepal-like but smaller. *Sepals* ovate, somewhat variable in shape, c. 2 mm long, concave, very thin, scarious but with a median keel and a sulcate keel-tip, glabrous, irregularly setose-ciliate. *Corolla* 2,75 mm long subcampanulate-cyathiform, dry, glabrous, thin in texture, white; lobes about $\frac{1}{3}$ the length of the corolla, more or less continuous but, at maturity, probably spreading or recurved, subobtuse. *Filaments* ligulate; anthers included, 1 mm long, lateral, oblong, bipartite, muticous. *Ovary* subturbinate to globose, sparsely villous above; style included; stigma manifest, cyathiform, large.

Distribution. CAPE—3322 (Oudtshoorn): Swartberg range, Blesberg feature, Southern slopes, 1830 m (—BC), 17/10/1955, *Esterhuysen 24913* (holotype BOL, isotypes NBG, PRE, STE).

Flowers in spring.

Erica costatisepala H. A. Baker, sp. nov. (Ericaceae-Ericoideae) Trigemma.

Fruticulus erectus lignosus ad circa 23 cm altus. *Rami* numerosi, glabri et cicatricibus foliorum delapsorum notati. *Folia* 3—nata, 2—3 mm longa, erectipatentia, imbricata, navicularia, acutata, superne concava, obsure sulcata, glabra, primo ciliolata, pro parte majore ad basibus. *Flores* terminales, 3—nati,

calycini, pauci; pedunculi 3 mm longi, saepi curvi, glabri; bracteae remotae, 2—3 mm longae, lanceolateae, concavae. Sepala 3 mm longa, ovatolanceolata, concava, costa mediana distincta, glabra, scariosa, apicibus sulcatis. *Corolla* 3,25 mm longa, anguste cyathiformis, sicca, glabra, eburnea vel alba; lobis 1,2 mm longis, continuis, acutatis. *Filamenta* linearia; antherae inclusae vel inter lobi manisfestae, 1 mm longae, subterminales, anguste oblongae, bipartitae, scabrae, appendiculatae, poro fere dimidio lobi; cristae circa 0,25 mm longae, pendens, super bases loborum affixae, latae, decrescens et ad bases acutae, plus minusve incisae et irregululares. *Ovarium* turbinatum, atum, canovillosopubescentum; stylo exserto; stigmate capitellato, 4—lobato.

Erect, woody to about 23 mm in height. *Branches* many, glabrous, leafy, later bare and scarred with the persistent leaf cushions. *Leaves* 3—nate, 2—3 mm long, erect-spreading, imbricate, boat-shaped, acute, very concave above, obscurely sulcate, glabrous, ciliolate on the lower margins when young. *Flowers* 3—nate, terminal, calycine, few; peduncles 3 mm long, curved, glabrous; bracts remote, lanceolate, concave, 2—3 mm long. Sepals 3 mm long, ovate-lanceolate, concave, with conspicuous median midrib and sulcate tip, scarious, glabrous. *Corolla* 3,25 mm long, narrow-cyathiform, dry, glabrous, cream to white; lobes continuous, 1,25 mm long, acute. *Filaments* linear; anthers included to manifest between the lobes, 1 mm long, subterminal, linear-oblong, bipartite, scabrous, appendiculate; pore $\frac{1}{2}$ as long as the cell; crests about $\frac{1}{4}$ mm. long, pendulous, broad, tapering to a point, more or less deeply incised and irregular in shape. *Ovary* turbinate, dark in colour, white-villous-pubescent; style exserted; stigma capitellate, 4-lobed.

Distribution. CAPE 3321 (Ladismith): Rocky clefts and crevices on the highest parts of the Swartberg, Toverkop (—AC/AD), at 2072 m, 7 Dec, 1956, *Esterhuysen 26756* (holotype BOL, isotypes NBG, PRE, STE); 7 Weeks Poort (—AD), Dec. 1956, *Stokoe 7863/4* (BOL), *H. Andreae 1180* (BOL).

Flowering season, Midsummer.

Erica keeromsbergensis H. A. Baker, sp. nov. (Ericaceae-Ericoideae) Trigemma.

Fruticulus erectus, humilis, ramosus. *Rami* graciles, ramulis numerosis, pubescentes, glabrescens et cicatricibus foliorum delapsorum notari. *Folia* 3—nata, c. 1 mm longa, erectopatentia, imbricata, ovales, acutata, crassa, obscure sulcata, glabra. *Flores* terminales, 3—nati, calycini, pauci; pedunculi 2,5 mm longi, canopubescentes; bracteae approximatae, 1,5 mm longae, sepaloidae sed parviorae et angustiorae. *Sepala* 1,5 mm longa, variabiles, ovata vel ovales vel subovata, concava, plus minusve carinata, apicibus sulcatis, glabra, scariosa, parce ciliata setis caducis. *Corolla* 2,5 mm longa, anguste cyathiformis, sicca, glabra, alba; lobis 1,25 mm longis, continuis, subacutatis. Filamenta sursum decrescens; antherae inclusae, 0,75 mm longae, laterales,

late cuneatae, bipartitae sed non effusae, parce scabridae, aristatae; poro fere dimidio lobi; aristae circa $\frac{3}{8}$ mm longae, aliquantum effusae, anguste subulatae, ciliatae, pallidae. *Ovarium* globosum, glabrum; stylo multo-exserto, demum seaepe decurvo; stigmate capitellato, parvulo.

Dense, erect, low, twiggy shrub. *Branches* slender, pubescent, glabrescent and marked by the scars from the fallen leaves. *Leaves* 3—nate, about 1 mm long or a little more, erect-spreading, imbricate, oval, acute, thick, obscurely sulcate, glabrous, ciliolate. *Flowers* terminal, 3—nate, calycine; few; peduncules 2,5 mm long, white-pubescent; bracts approximate to subapproximate, 1,5 mm long, sepal-like but smaller and narrower. *Sepals* 1,5 mm long, variable in shape from ovate to oval or obovate, more or less keeled, sulcate-keel-tipped, scarious, glabrous, setose-ciliate. *Corolla* 2,5 mm long, narrow-cythiform, dry, glabrous, white; lobes continuous, 1,25 mm long, subacute. Filaments tapering upwards; anthers included, $\frac{3}{4}$ mm long, lateral, oblong-cuneate, slightly scabrid, bipartite but not spreading, awned, pore about half as long as the cell; awns about half as long as the cells, slightly spreading, narrow-subulate, ciliate, pale. *Ovary* globose, glabrous; style long-exserted and often deflected; stigma capitellate, small.

Flowering season, autumn.

DISTRIBUTION. CAPE—3319 (Worcester): Ben Heatlie on Keeromsberg (—DA), among sand against rocks close to the summit at 1960 m, 22 March 1958, *Esterhuysen 27647* (holotype BOL, isotypes NBG, PRE, STE).

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The author wishes to thank Professor W. P. U. Jackson for collecting and bringing to his notice the material of the species named *E. altevivens* and to the curators and staff of Bolus and Compton herbariums for much valuable advice and assistance.

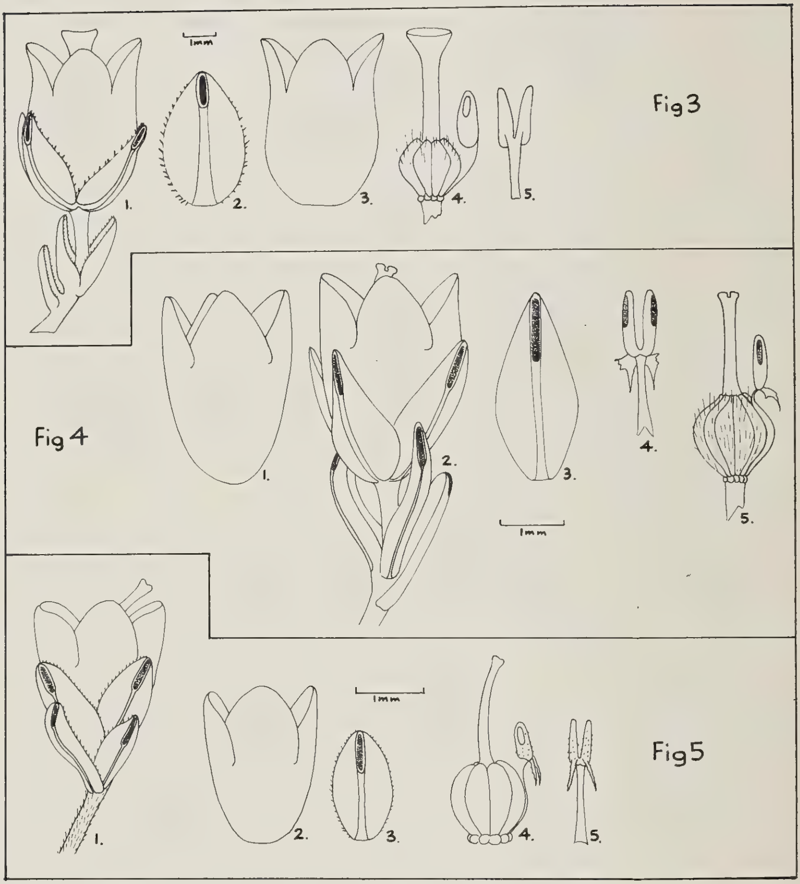

FIG. 3.
Erica blesbergensis H. A. Baker. 1. Flower; 2. Sepal, spread out; 3. Corolla; 4. Gynoecium and stamen; 5. anther, back view. *del. H. A. Baker.* By Mrs. De Moor.

FIG. 4.
Erica costatisepala H. A. Baker. 1. Corolla; 2. Flower; 3. Sepal; 4. Anther, front view; Gynoecium and stamen. *del. H. A. Baker.* By Mrs. De Moor.

FIG. 5.
Erica keeromsbergensis H. A. Baker.1. Flower; 2. Corolla; 3. Sepal; 4. Gynoecium; 5. Anther, back view. By Mrs. De Moor.

C.T.P. LTD.

Jl S. Afr. Bot. 37 (3): 177–182 (1971)

TERENCE MACLEANE SALTER (1883–1969)

Terence Macleane Salter was born on the 5th of February 1883 at Cheltenham, in the county of Gloucestershire and died in Cape Town on the 30th of March, 1969. His ashes were scattered at sea in Table Bay by officers of the Royal Navy from H.M.S. Juno. His father was James Colam Salter, a college master and his mother Emily Susanna Salter (née Wilding). Captain Salter's love of plants and skill as a botanical illustrator came through a family interest and involvement. His grandfather, John William Salter (1820–1869) was apprenticed to James de Carle Sowerby, second son of the illustrator of the great 36 volume work, Sowerby's *English Botany*, and in 1846 he married Sally Sowerby, second daughter of James Sowerby, the younger.

At the age of 17, Terence Salter joined the Royal Navy and on the 5th February, 1904 was commissioned in the Paymaster's office at Malta. Captain Salter remained a paymaster until his retirement from the Royal Navy in 1931. He served in many famous ships including H.M.S. Glory, Diligence, Hood, Defiance, Impregnable and was on H.M.S. Lowestoft when he was first stationed at Simonstown. It was at Simonstown that he was introduced to the Cape Flora, a flora which was to occupy so much of his time in the years ahead. On his retirement in 1931, Salter devoted the remainder of his active life to the study of the Cape Flora although he had started his private herbarium in 1927. By nature a solitary man, Captain Salter never married, but nevertheless found much pleasure in the company of other botanists although in his later years increasing deafness made conversations with him almost impossible.

During the period 1927–1929, Captain Salter made his first collections on the Cape Peninsula. These are recorded in a special book in which the pages and species are numbered to correspond with Bolus' and Wolley-Dod's *List of the Flowering Plants and Ferns of the Cape Peninsula*. The major part of this collection was presented to the British Museum, the remainder to Kew. The numbering of his main set of collecting registers (in 4 volumes) is explained by Salter himself in a note on the first page of vol. I: "The series of numbers commencing on the 30th April 1931 was opened from 501 in order to prevent any confusion with the previous numbers in my first note book viz. 231/1 to 385/5". These collecting numbers from 501 to 9812 covering the period 30th April, 1931 to 5th December, 1957 have marginal symbols indicating the different institutions to which the specimens were distributed. (These were BOL, K, BM, SAM, NBG, CT, LD). The number of duplicates of *Oxalis* specimens

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distributed (including his personal collection of *Oxalis* now in the Compton Herbarium) was 5660, distributed among the following institutions: B, BM, BOL, K, NBG, MO, PRE, TRV (now incorporated in PRE), SAM, UPS, and W. (Abbreviated according to *Index Herbariorum*, 1964). All his collecting registers are preserved in the Compton Herbarium together with his botanical library which he presented to Kirstenbosch shortly before his death.

Captain Salter was primarily a field worker—a keen observer of minute details. He believed that taxonomic problems could only be satisfactorily resolved with a thorough knowledge of the living plants gained by personal field experience. His meticulously prepared herbarium material enriched with his own observations bears testimony to this. It is therefore not surprising that he had a rather bold approach to nomenclatural matters, at times showing a certain degree of impatience with scrappy but nevertheless historically important specimens. This "encumbrance of past inadequate work" as Salter called it, he was inclined to disregard. Although Captain Salter's taxonomic interests covered a wide range of families, notably *Ericaceae*, *Proteaceae*, *Droseraceae* and *Leguminosae*, he is best remembered for his massive monograph *The genus Oxalis in South Africa*, skilfully illustrated with his own pen. This work together with major contributions to the *Flora of the Cape Peninsula* of which he was co-editor with Prof. R. S. Adamson, rank as his greatest achievements. An excellent Latin scholar, he was always willing to lend a helping hand in drawing up Latin descriptions for those less well acquainted with the Latin language. His name is commemorated in several plants including *Saltera sarcocolla* (L.) Bullock, *Oxalis salteri* L. Bol., *Erica salteri* L. Bol., *Lachenalia salteri* Barker, and *Disa salteri* Lewis. Salter had a long association with the Bolus Herbarium and the National Botanic Gardens, Kirstenbosch. In 1939 he was made the first Honorary Reader in Systematic Botany at the Bolus Herbarium, a position which he held for 30 years. His contributions to South African Botany were further honoured when, in 1955, the University of Cape Town conferred on him the honorary degree of Doctor of Science.

But perhaps the most significant awards made to Captain Salter to recognise his achievements as an amateur, were the Certificate of Merit awarded by the South African Association for Advancement of Science in 1962, followed in 1965 by the Bolus medal, presented by the Botanical Society of South Africa. Of the latter award, he was the first recipient. These were indeed most fitting honours for the work of Captain Salter is an outstanding example of what taxonomic botany in South Africa owes to the gifted amateur.

E. P. du Plessis
J. P. Rourke

List of Paymaster-Captain T. M. Salter's Botanical Publications.

1930

Some new species of *Oxalis* from South Africa. *J. Bot., Lond.* **68:** 143–146, with A. W. Exell.

1935

Plantae Novae Africanae I *Jl S. Afr. Bot.* **1:** 32–39, with W. F. Barker & R. H. Compton.
Plantae Novae Africanae II *Jl S. Afr. Bot.* **1:** 75–86.
Plantae Novae Africanae III *Jl S. Afr. Bot.* **1:** 111–128, with R. H. Compton.
Plantae Novae Africanae IV *Jl S. Afr. Bot.* **1:** 129–152.

1936

Plantae Novae Africanae V *Jl S. Afr. Bot.* **2:** 1–18.
Plantae Novae Africanae VI *Jl S. Afr. Bot.* **2:** 47–64, with E. Esterhuysen.
Plantae Novae Africanae VII *Jl S. Afr. Bot.* **2:** 145–169, with A. A. Obermeijer, C. E. B. Bremekamp and R. H. Compton.
Some notes on hybridisation of Ericaceae in the Klaver valley at Simonstown. *Jl S. Afr. Bot.* **2:** 129–140.

1937

Plantae Novae Africanae VIII *Jl S. Afr. Bot.* **3:** 93–102, with W. F. Barker.
Notes on some species in the family Rubiaceae in the Cape Peninsula. *Jl S. Afr. Bot.* **3:** 109–116.
Oxalis helicoides. Flower. Pl. S. Afr. Plate 579.

1938

Plantae Novae Africanae IX *Jl S. Afr. Bot.* **4:** 13–20.
Plantae Novae Africanae X *Jl S. Afr. Bot.* **4:** 109–122.

1939

Some changes in nomenclature Series 11. *Jl S. Afr. Bot.* **5:** 58, with R. S. Adamson, F. M. Leighton.
Plantae Novae Africanae XI and XII. *Jl S. Afr. Bot.* **5:** 41–74.
Amalgamation of the genus *Hallia* Thunb. and *Psoralea* L. *Jl S. Afr. Bot.* **5:** 45–46.
Some notes on the correct identity of *Oxalis pes-caprae* L. and *Oxalis purpurea* L. *Jl S. Afr. Bot.* **5:** 47–52.
Notes on some of the species of *Drosera* occurring in the Cape Peninsula, including the new species *D. glabripes* (Harv) Salter and *D. curviscapa* Salter. *Jl S. Afr. Bot.* **5:** 157–162.

1940

Plantae Novae Africanae Series XIII. *Jl S. Afr. Bot.* **6:** 1–54, with E. Esterhuysen.
Plantae Novae Africanae Series XV. *Jl S. Afr. Bot.* **6:** 165–167.
Some notes on S. African *Oxalis* section *Cernuae. Jl S. Afr. Bot.* **6:** 11–20.
Some notes on nomenclature, generic definition and the species question in the genus *Sarcocolla. Jl S. Afr. Bot.* **6:** 41–44.
Some notes on the confusion between *Oxalis reclinata* Jacq. and *Oxalis gracilis* Jacq. *Jl S. Afr. Bot.* **6:** 121–126.
Notes on *Pelargonium multiradiatum* Wendl. *Jl S. Afr. Bot.* **6:** 127–130.
Oxalis polyphylla Jacq. *Jl S. Afr. Bot.* **6:** 191–194.

1941

Plantae Novae Africanae XVI. *Jl S. Afr. Bot.* **7:** 77–87, with M. R. Levyns, E. Esterhuysen & G. J. Lewis.
Some notes on the species of *Eriospermum* which occur in the Cape Peninsula. *Jl S. Afr. Bot.* **7:** 103–114.
Some notes on *Oxalis crispula* Sond. & *Oxalis stenoptera* Turcz. *Jl S. Afr. Bot.* **7:** 153–158.
A new variety of *Oxalis imbricata* E. & Z. with notes on the confusion between *O. imbricata* and *O. zeekoevleyensis* R. Knuth. *Jl S. Afr. Bot.* **7:** 159–162.
Notes on *Oxalis pulchella* Jacq. and its varieties. *Jl S. Afr. Bot.* **7:** 162–168.

1942

Plantae Novae Africanae XVIII *Jl S. Afr. Bot.* **8:** 245–270, with W. F. Barker, R. H. Compton, S. Garside, M. R. Levyns and G. G. Smith.

Some changes in Nomenclature III *Jl S. Afr. Bot.* **8:** 271–284, with R. S. Adamson, M. R. Levyns and E. P. Phillips.

1943

Some notes on the genus *Leucadendron*, with descriptions of new species. *Jl S. Afr. Bot.* **9:** 1–19.

Some notes on *Oxalis meisneri* Sond. and *Oxalis cana* Sond. *Jl S. Afr. Bot.* **9:** 160–163.

1944

Plantae Novae Africanae XXII *Jl S. Afr. Bot.* **10:** 55–60, with F. M. Leighton.

The genus Oxalis in South Africa. A taxonomic revision. Supplementary Vol. No. 1 *Jl S. Afr. Bot.*

1946

Plantae Novae Africanae XXV *Jl. S. Afr. Bot.* **12:** 35–42, with R. S. Adamson, J. Gerstner.

Some notes on the genus *Hermannia* with description of 5 new species *Jl S. Afr. Bot.* **12:** 95–103.

1948

Oxalis laburnifolia Jacq. and its status as a species, with a description of a new variety and (II) notes on the aerial bulbils of *O. laburnifolia. Jl S. Afr. Bot.* **14:** 13–16.

1949

Plantae Novae Africanae XXIX *Jl S. Afr. Bot.* **15:** 35–42, with G. J. Lewis and W. F. Barker.

1950

Oxalis salteri. Flower. Pl. Afr. Plate 1094.

Flora of the Cape Peninsula. Juta & Co. Ltd. Cape Town and Johannesburg: (Editors R. S. Adamson & T. M. Salter).

1951

Notes on the process of forming contractile roots and the lowering of the first bulbils by seedlings of the S.A. oxalis which produce endospermous seeds. *Jl S. Afr. Bot.* **18:** 189–194.

1953

A note on sex in *Royena glabra* L. *Jl S. Afr. Bot.* **19:** 29–30.

1956

A new marsh *Erica* from Wemmershoek. *Jl S. Afr. Bot.* **22:** 37–40.

1957

Notes and Errata to Journal of South African Botany Supp. Vol. 1. "The genus *Oxalis* in S.A." *Jl S. Afr. Bot.* **23:** 103–104.

1958

Oxalis flava. Flower. Pl. Afr. Plate 1266.

Oxalis caprina & O. dentata. Flower. Pl. Afr. Plate 1267.

Oxalis incarnata. Flower. Pl. Afr. Plate 1275.

Oxalis lanata & O. commutata. Flower. Pl. Afr. Plate 1276.

Oxalis luteola. Flower. Pl. Afr. Plate 1277.

1959

Volume 33 of Flowering Plants of Africa dedicated to Captain Salter. *Oxalis bifida & O. natans. Flower. Pl. Afr.* Plate 1284.

Oxalis nidulans & O. minuta. Flower. Pl. Afr. Plate 1285.

Oxalis hirta. Flower. Pl. Afr. Plate 1297.

Oxalis tenuifolia & O. versicolor. Flower. Pl. Afr. Plate 1298.

Oxalis polyphylla, O. punctata & O. monophylla. Flower. Pl. Afr. Plate 1303.

1960

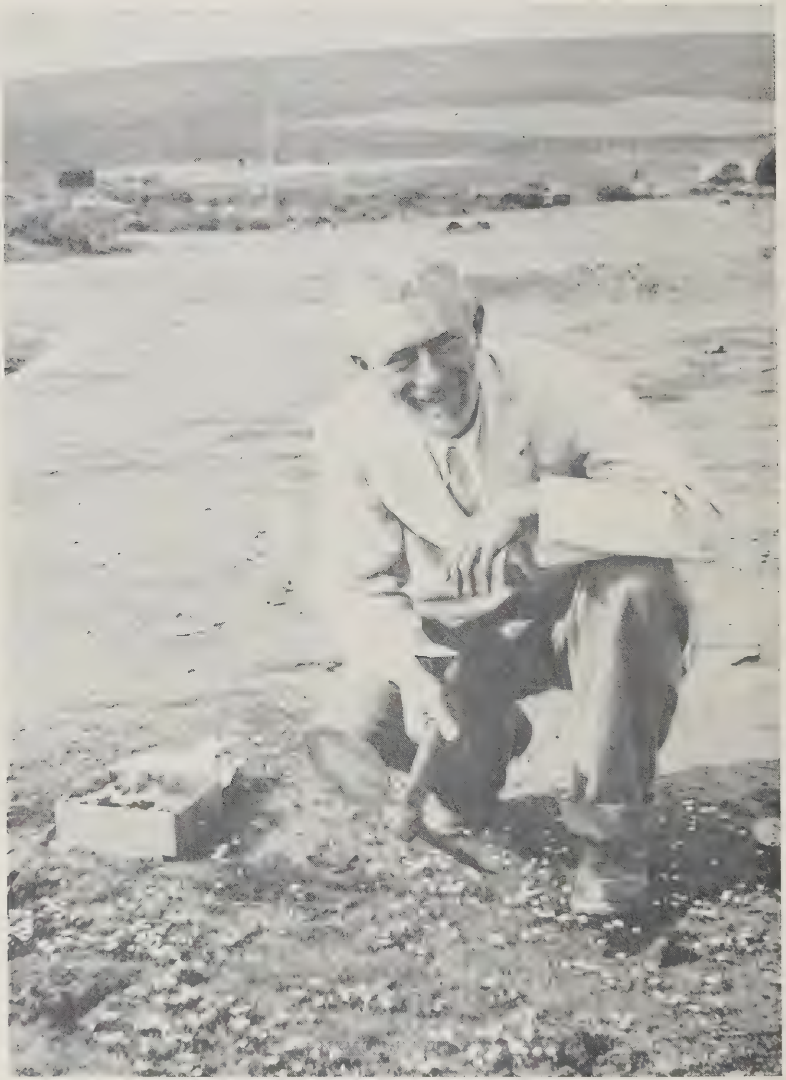
Oxalis purpurea. Flower. Pl. Afr. Plate 1323.
Oxalis eckloniana var. *sonderi. Flower. Pl. Afr.* Plate 1324.

1961

Oxalis glabra & O. pusilla. Flower. Pl. Afr. Plate 1336.
Oxalis falcatula & O. multicaulis. Flower. Pl. Afr. Plate 1337.
Oxalis polyphylla var. *pentaphylla & Oxalis obtusa. Flower. Pl. Afr.* Plate 1349.

1962

Oxalis pes-caprae. Flower. Pl. Afr. Plate 1362.
Oxalis pes-caprae var. *sericea. Flower. Pl. Afr.* Plate 1363.
Oxalis compressa. Flower. Pl. Afr. Plate 1364.



TERENCE MACLEANE SALTER (1883—1969)
CAPTAIN R.N., HON. D.SC.

C.T.P. LTD.

Jl S. Afr. Bot. 37 (3): 183–188 (1971)

A NEW SPECIES OF *PROTEA* FROM THE SOUTH EASTERN CAPE

J. P. Rourke

(*Compton Herbarium, Kirstenbosch*)

ABSTRACT

A new species of dwarf *Protea, Protea intonsa* Rourke, is described.

UITTREKSEL

'N NUWE SOORT *PROTEA* VAN DIE SUID-OOS-KAAP.
'n Nuwe soort dwerg *Protea, Protea intonsa* Rourke, word beskryf.

INTRODUCTION

Several collections of a dwarf caespitose species of *Protea* from the mountains of the south eastern Cape have been made during the past 30 years. This material, deposited in a number of South African herbaria, could not be identified with any previously published description of *Protea.* A careful examination of the type material of all possible allied taxa confirmed the view that these collections represented a hitherto undescribed species.

Protea intonsa Rourke, sp. nov.

Haec species caespitosa, a foliis glabris acicularibus canaliculatis vel linearibus, 15–40 cm longis, 2–5 mm latis, et perianthio, glabro praeter perianthium limbum manifeste lanatum ad apicem, distinguitur.

Fruticulus nanus, caespitosus, 30–60 cm in diam., 15–40 cm altus. *Caules* breves, hypogaei. Ramuli caespites terminales foliorum ferentes. *Folia* acicularia canaliculata vel linearia, 15–40 cm longa, 2–5 mm lata, glabra, laevia vel leviter scabra. *Inflorescentiae* globosae cyathiformes, 2–5 cm in diam. *Receptaculum involucrale* 1–2 cm in diam., planum. *Bracteae* involucrales 4–5 seriatae, minutae et sparsae sericeae, glabrescentes. Series intima oblonga spathulata, 2–2,5 cm longa, 1 cm lata, apices rotundatos concavos. Series externa ovata obtusa, 1–1,5 cm lata. *Perianthium* 2,5–3 cm longum, glabrum praeter perianthium limbum, manifeste lanatum ad apicem. Perianthium limbi lineares, acuminati, glabri sed apices dense lanatos. Limbus medianus adaxialis brevior quam alteri. *Stylus* 2,5–3 cm longus, arcuatus adaxialis, contractus terminalis, leviter quadrangulatus compressus. *Stigma* peranguste lineare vel filiforme, 5–6 mm longum, compressum, longistrorsum sulcatum.

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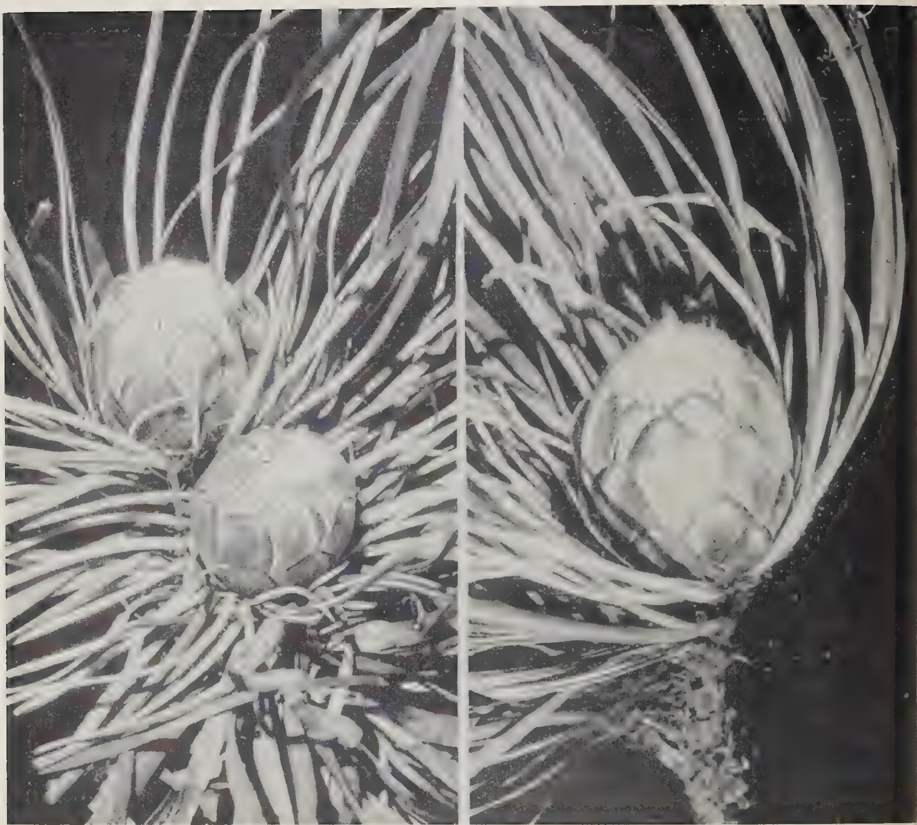

FIG. 1.

Protea intonsa showing the inflorescences at anthesis. Slightly less than life size. (Part of the type material, *J. P. Rourke 860*.)

A dwarf tufted shrublet forming clumps 30–60 cm in diam., 15–40 cm in height. *Branches* short, subterranean; terminal branchlets bearing tufts of leaves at or just above soil level. Subterranean branches bearing alternately arranged lanceolate to ovate scales. *Leaves* acicular canaliculate to linear, 15–40 cm long, 2–5 cm wide, glabrous except for a few slender trichomes in the petiolar region, occasionally slightly glaucous, smooth to slightly scabrous, apex acute to mucronate. *Inflorescences* globose cyathiform 2–5 cm in diam. *Involucral receptacle* 1–1,5 cm in diam., flat. *Involucral bracts* 4–5 seriate, the innermost

series oblong spathulate, 2–2,5 cm long, 1 cm wide, apices broadly obtuse, slightly concave; the outer series broadly ovate, 1–1,5 cm long, 1–1,5 cm wide; outer surface of bracts minutely and sparsely sericeous soon becoming glabrous, margins minutely ciliate; greenish, flushed with dull carmine becoming more uniformly carmine with age. *Perianth* 2,5–3 cm long, glabrous except for the densely lanate apices of the perianth limbs. Adaxial perianth sheath 4 mm wide proximally tapering to filiform below the perianth limbs, margins undulate and involute. Free perianth segment 1,5 mm wide proximally, tapering to filiform below the limb. *Perianth limbs* linear acuminate, 7–9 mm long glabrous for greater part of their length except for the densely lanate apices; median adaxial limb shorter than the rest. *Anthers* 4–5 mm long, linear, terminated by an ovoid to saggitate apical boss. *Style* adaxially arcuate, 2,5–3 cm long, tapering subterminally, slightly quadrangular, compressed, glabrous. *Pollen presenter* narrowly linear to filiform, flattened, 5–6 mm long, longitudinally grooved, apex rounded. *Hypogynous scales* ovate acute to irregularly oblong, retuse to bifid, 1,5 mm long, 1 mm wide.

Diagnostic Characters: Protea intonsa is distinguished by its compact caespitose growth habit, its long, glabrous, acicular canaliculate to linear leaves, 15–40 cm long, 2–5 cm wide, and the perianth, completely glabrous except for the thickly lanate apices of the perianth limbs. In the young inflorescence just before anthesis, the prominent white beard which projects a distance of up to 7 mm from the innermost series of involucral bracts, is a very marked distinguishing character.

The overall morphological features of *P. intonsa* suggest an affinity with *P. montana* E. Mey. ex Meisn. Both species have been observed growing sympatrically on Mannetjiesberg in the Uniondale district but no evidence of hybridization was found.

Type Material: Uniondale district, Mannetjiesberg, south slopes, 18/9/1967, *J. P. Rourke 860*, holotype NBG, isotypes PRE, STE.

Specimens Examined:

CAPE PROVINCE—3322 (Oudtshoorn): Blesberg, Swartberg Range, north slopes, (-BC), 17/10/1955, *Esterhuysen 24927* (BOL); Mannetjiesberg, south slopes, (-DB), 18/9/1967, *Rourke 860* (NBG, PRE, STE); Mannetjiesberg, south east ridge, 19/9/1954, *H. C. Taylor 1471* (NBG).

—3323 (Willowmore): Anthoniesberg, south slopes, (-AD), 19/10/1955, *Esterhuysen 24936* (BOL); Slypsteenberg, south slopes, (-AD), 3/11/1941, *Esterhuysen 6350* (BOL).

—3324 (Steytlerville): On south facing ridge of Scholtzberg, sloping towards Baviaanskloof, (-CB), 2/9/1962, *B. P. Loots s.n.* (PRE); Scholtzberg, Baviaanskloof mountains, south slopes of lowest ridge peak, 24/9/1953, *H. C. Taylor* 950 (NBG).

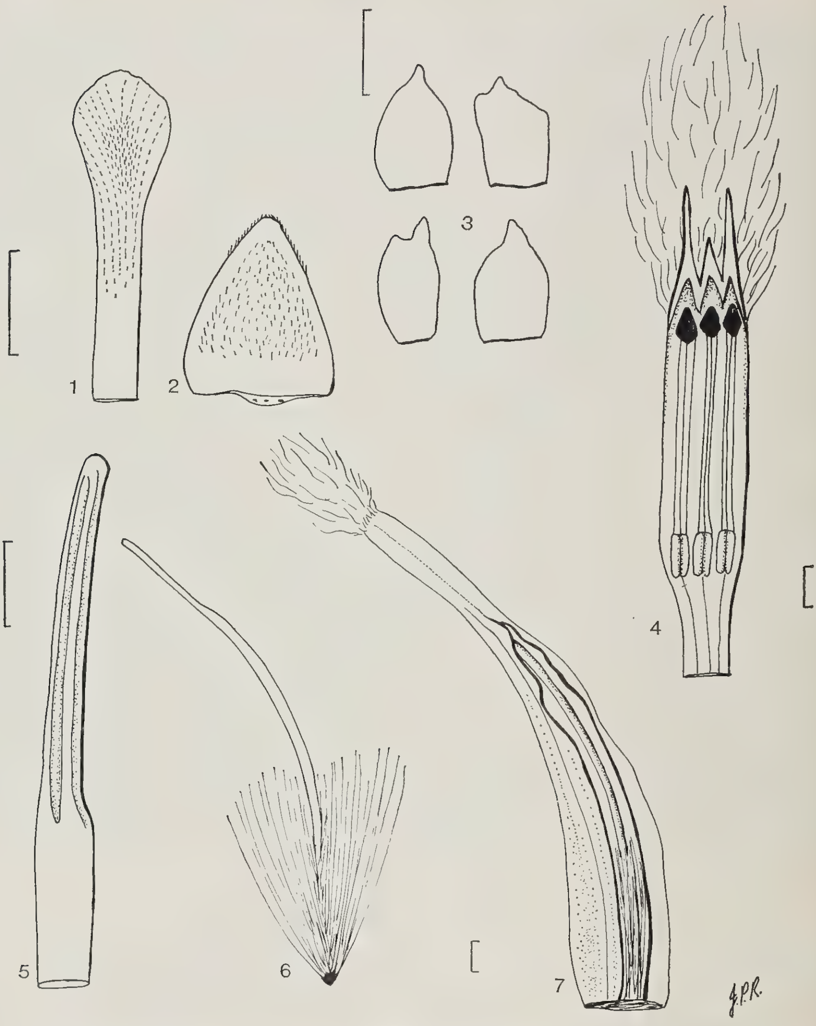

FIG. 2.

Diagrams of the floral parts of *Protea intonsa.* (1) Involucral bract of the innermost series; (2) involucral bract of the outer series; (3) hypogynous scales showing their irregular form; (4) adaxial perianth limbs showing the anthers, the shorter median adaxial perianth limb and the lanate apices of the perianth limbs; (5) pollen presenter; (6) gynoecium; (7) perianth before anthesis showing the lanate apices of the perianth limbs. The scale lines represent 1 mm.

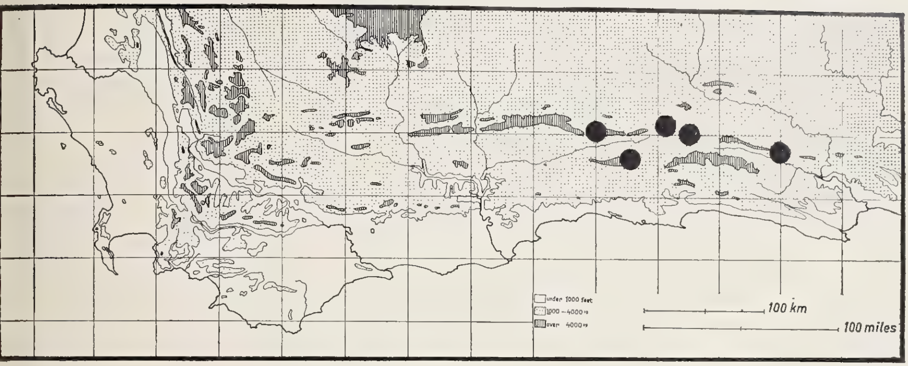

FIG. 3.
Distribution range of *Protea intonsa.*

DISCUSSION

Protea intonsa appears to be confined to a few high peaks on the inland mountain ranges of the south eastern Cape. The most westerly records are from Blesberg on the Swartberg range and the most easterly are from Scholtzberg, at the eastern end of the Baviaanskloof mountains. Populations have been observed at several localities in the Kammanassie mountains where it is fairly abundant locally. To date, this species has only been recorded at elevations of 1 000–1 500 m above sea level. *P. intonsa* thrives in hot, dry, exposed habitats, on rocky slopes of Table Mountain Sandstone in either north or south facing situations, where the mean annual rainfall is 250–375 mm p.a. (±10–15″).

The mature plants are very fire resistant. New shoots regenerate from the subterranean stems within a few months after the aerial stems have been burnt off. Flowering commences in September and continues until November. On opening, the involucral bracts are greenish tinged with carmine but as the inflorescence ages the bracts become more uniformly flushed with dull carmine. During November 1970 several populations in the Kammanassie mountains were studied but in all the specimens inspected it was found that the developing inflorescences had reached a diameter of about 1 cm and then aborted. Inflorescence development was probably arrested as a result of the prolonged drought of 1969–1970, which was one of the most severe droughts experienced in the Cape for several decades.

Jl S. Afr. Bot. 37 (3): 189–198 (1971)

TWO NEW SPECIES OF *COMMIPHORA* JACQ.

J. J. A. van der Walt

(*Botany Department, University of Stellenbosch*)

ABSTRACT

Commiphora cervifolia and *C. gracilifrondosa* are described. *C. cervifolia* was discovered recently. *C. gracilifrondosa* was incompletely described by Dinter. The possible relationships of the two species are indicated.

UITTREKSEL

TWEE NUWE SOORTE *COMMIPHORA* JACQ.
Commiphora cervifolia en *C. gracilifrondosa* word beskryf. *C. cervifolia* is onlangs vir die eerste keer ontdek, terwyl *C. gracilifrondosa* vroeër onvolledig deur Dinter beskryf is. Die moontlike verwantskappe van die twee spesies word ook aangedui.

Commiphora cervifolia Van der Walt, species. nova, *C. capensis* (Sond.) Engl. habitu, foliis trifoliolatis, absentia pseudarilli affinis, sed ab eo foliolis cultratis et irregulariter lobatis, petalis parvis, ramulus crassis et brevibus differt.

Frutex dioecius as 2 m altus. *Truncus* ramificans iterum atque iterum super planum soli, facie succulenta; ramuli multi breves et crassi. *Folia* trifoliolata ad 1,5 cm longa; foliola parva cultrata et irregulariter lobata. *Flores* unisexuales perigyni. *Calyx* carnosus et glandulosus. *Petala* parva. *Fructus* ellipsoideus, assymetrice complanatus, sine pseudarillo.
Type: Cape, 8 km S. of Vioolsdrif, *Van der Walt* 128 (PRE, holo; PRU).

Dioecious shrub up to 2 m high. *Trunk* branching repeatedly above soil level, appearing succose, with numerous short, stout, glandular side branches; bark grey-green to yellow-brown with dark patches. *Leaves* trifoliolate, up to 1,5 cm long, sparsely glandular; petiole up to 5 mm long; leaflets small, cultrate, mostly irregularly lobed, apex acute to obtuse, base cuneate, margins entire irrespective of lobes; terminal leaflet up to 1 × 0,2 cm; lateral leaflets up to 0,8 × 0,2 cm. *Flowers* unisexual, perigynous, appearing before the leaves, solitary or in axillary dichasial cymes up to 2 cm long; male flowers, 6—7 mm, usually larger than female flowers, 5—6 mm. *Bracts* up to 0,5 mm long lanceolate, sparsely glandular. *Pedicels* 1—1,5 mm long, sparsely glandular. *Calyx* yellow-green to brown. 1,7—2,2 mm long, fleshy, broadlyc ampanulate, continuous with hypanthium, sparsely glandular, lobes up to 2 mm long, apex

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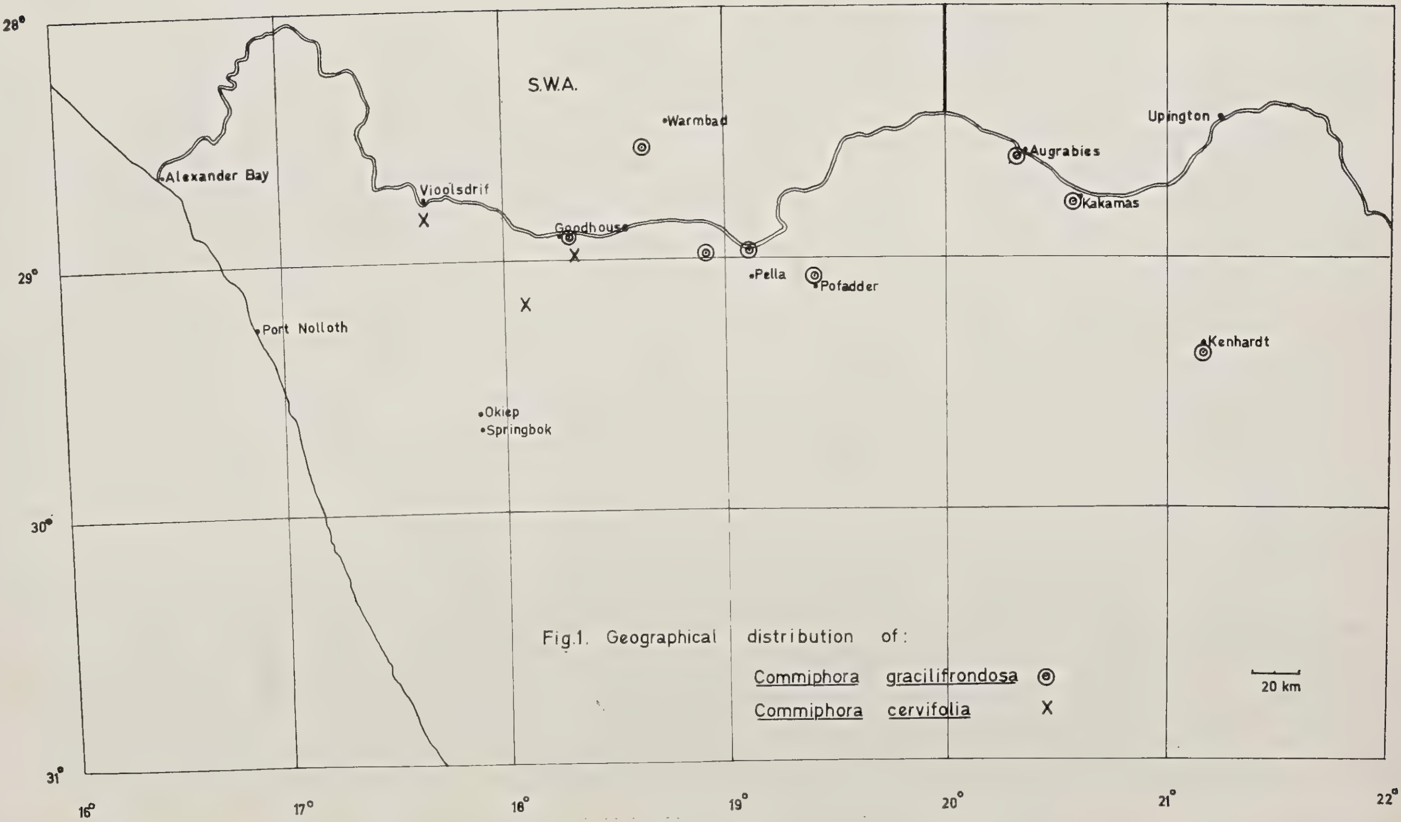

Fig.1. Geographical distribution of:
<u>Commiphora</u> <u>gracilifrondosa</u> ◎
<u>Commiphora</u> <u>cervifolia</u> X

acute. *Petals* yellow-green to brown, 2—3 mm long. *Disc* forming 4 fleshy lobes, fused with hypanthium. *Stamens* 8, 4 up to 3 mm long, 4 up to 2,2 mm long; filaments slender, subterete, lower part flattened and broadened; staminodes

Fig. 2.
Commiphora cervifolia, on farm "Geselskapbank", near Goodhouse (height 0,5 m).

in female flowers. *Gynoecium* rudimentary in male flowers; ovary sparsely glandular; style short, sparsely glandular; stigma obscurely 4-lobed. *Fruit* 1,1 × 1 cm, ellipsoid, asymmetrically flattened; exocarp smooth; mesocarp thin; endocarp smooth, 9 × 8 mm, ellipsoid, asymmetrically flattened with one face rather deeply convex and one shallowly convex, without pseudaril.

Diagnostic features: Dioecious shrub. Trunk branching repeatedly above soil level, appearing succose, with numerous short, stout side branches. Leaves trifoliolate up to 1,5 cm long, leaflets small, cultrate, irregularly lobed. Flowers perigynous, calyx fleshy and glandular, petals small. Fruit ellipsoid, without pseudaril.

The species is apparently confined to the semi-desert areas of the N. W. Cape from Goodhouse in the east to Vioolsdrif in the west. No material could be

traced in any of the South African herbaria to verify further occurrences of the species geographically. A photograph of the leaves was sent to Merxmüller, but he declared that he had never seen material collected in S.W.A. It occurs at the foot or on the slopes of the arid mountains or koppies in the vicinity of the Orange River in areas with an annual rainfall of less than 80 mm.

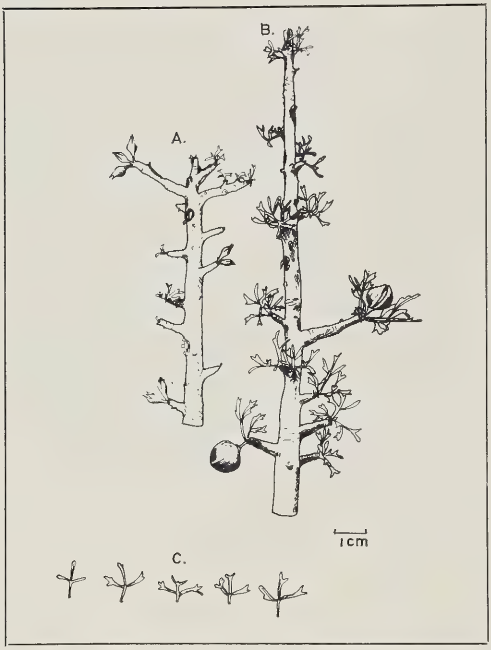

FIG. 3.
Commiphora cervifolia.
A, branchlet with young leaves and inflorescences.
B, branchlet with leaves and fruits.
C, leaves.

CAPE.—2817 (Vioolsdrif): 8 km S. of Vioolsdrif (-DC), *Van der Walt* 128 (PRE; PRU). 2818 (Warmbad): 13 km S.E. of Goodhouse (-CD), *Van der Walt* 115 (PRE; PRU). 2918 (Gamoep): 56 km N.E. of Okiep on farm Geselskapbank (-AA), *Van der Walt* 123 (PRE; PRU).

C. cervifolia is probably closely related to *C. capensis* (Sond.) Engl. The two species have many characteristics in common, especially as far as growth form, external features of the stems and fruits are concerned. Although both species have trifoliolate leaves, the form of the leaflets differs considerably. The leaflets of *C. capensis* are rotund or obovate or cordate with finely lobed margins. The calyx of *C. cervifolia* is more fleshy than that of *C. capensis* while the petals are smaller than those of the latter species.

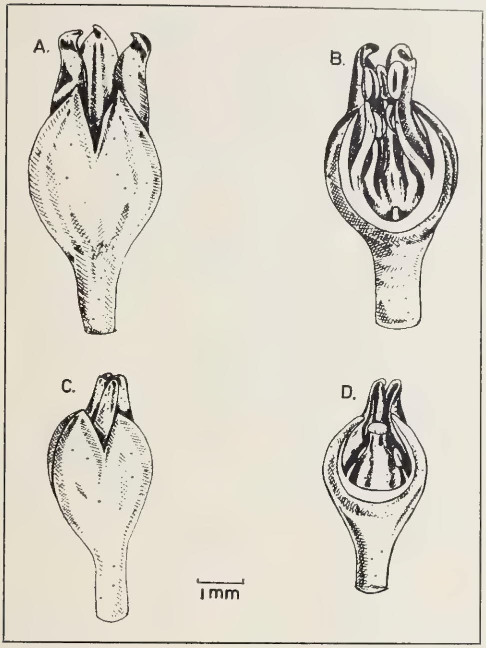

FIG. 4.
Commiphora cervifolia.
A, male flower.
B, longitudinal section of male flower.
C, female flower.
D, longitudinal section of female flower

Living shoots, on being touched, exude an aromatic secretion in such quantities that the stems become wet. The form of the leaflets with the irregular lobes, resembles the antlers of a stag hence the name of the species.

Commiphora gracilifrondosa Dinter ex Van der Walt, species nova (Dinter in Feddes Rep. Beih. 53: 48 (1928), nomen subnudum), *C. oblanceolata* Schinz habitu, foliis trifoliolatis et stminibus quatuor affinis, sed ab eo foliis majoribus et petiolis longioribus, foliolis linearibus ad cultratis et marginibus irregulariter et paulo grosse dentato-serratis differt.

Frutex dioecious ad 3 m altus. *Truncus* ramificans iterum atque iterum super planum soli, facie succulenta; ramuli graciles. *Folia* trifoliolata ad 6 cm longa; foliola variabilia linearia ad cultrata marginibus irregulariter et paulo grosse dentato-serratis. *Flores* unisexuales perigyni. *Calyx* sparsim glandulosus. *Stamina* vel *staminodia* quatuor. *Fructus* subglobosus ad ellipsoideus, asymmetrice complanatus; pseudarillus cupulatus duis brachiis.

Type: S.W.A., Warmbad, near Auros, *Dinter* 5124 (BOL, holo; S!; B†).

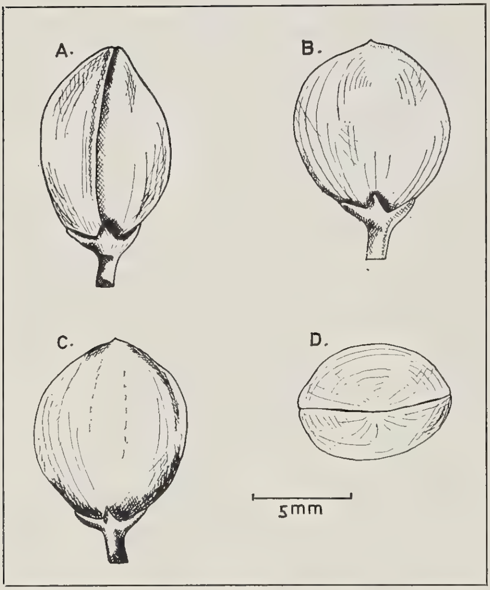

FIG. 5.
Commiphora cervifolia.
A, fruit.
B, deeply convex face of endocarp.
C, shallowly convex face of endocarp.
D, endocarp seen from apex.

Dioecious shrub up to 3 m high. *Trunk* branching repeatedly above soil level, appearing succose, young branches slender and glandular; bark red-brown with dark patches. *Leaves* trifoliolate but terminal leaflet sometimes 3-lobed, up to 6 cm long, sparsely glandular; petiole up to 2 cm long, sparsely glandular; petiolules up to 3 mm long; leaflets variable in size and form, linear to cultrate, margins irregularly and rather coarsely dentate-serrate, apex obtuse to acute, base cuneate; terminal leaflet up to 4,3 × 0,2 cm, lateral leaflets up to 3,5 × 0,2 cm. *Flowers* unisexual, perigynous, appearing before or with the leaves in axillary dichasial cymes or occasionally solitary, branches of inflorescence sparsely glandular, male inflorescence up to 5 cm long, female inflorescence up to 1 cm long; male flowers, 6—7 mm, usually larger than female flowers, 4—5 mm. *Bracts* up to 4 mm long, linear, sparsely glandular. *Calyx* yellow-green. 1,2—1,5 mm long, campanulate, continuous with hypanthium, sparsely glandular, lobes up to 1 mm long, apex acute. *Petals* yellow-green, 2,5—3,5 mm long. *Disc* forming 4 fleshy lobes, fused with hypanthium. *Stamens* only 4, up to 2,5 mm long, inserted on disc-lobes; filaments slender, subterete, lower part flattened and broadened; anthers relative large; staminodes in female flowers. *Gynoecium* rudimentary in male flowers; ovary sparsely glandular; style long, sparsely glandular; stigma obscurely lobed. *Fruit* 1 × 0,8 cm,

FIG. 6.
Commiphora gracilifrondosa, near Pella (height 1,5 m).

subglobose to ellipsoid, asymmetrical, slightly flattened; exocarp smooth; mesocarp thin; endocarp smooth, 8 × 5 mm, ellipsoid, assymmetrically flattened with one face deeply convex and the other shallowly convex; pseudaril red, not very fleshy, cupular with 2 arms on ridge of stone, pseudaril covers the lower $\frac{1}{2}$ of the shallowly convex face of stone and the lower $\frac{1}{4}$ of the deeply convex face.

Diagnostic features: Dioecious shrub. Trunk branching repeatedly above soil level, appearing succose, young branches slender. Leaves trifoliolate up to 6 cm long, leaflets variable, linear to culture and the margins rather coarsely dentate-serrate. Flowers perigynous, stamens/staminodes 4. Fruit subglobose to ellipsoid, pseudaril cupular with 2 arms.

C. gracilifrondosa occurs in N.W. Cape with collections from Kenhardt in the east to Goodhouse in the west. It is also recorded from the southern part of S.W.A. It grows on the arid mountains and koppies in the vicinity of the Orange River in areas with an annual rainfall up to 160 mm.

S.W.A.—2818 (Warmbad): near Auros (-DA), *Dinter 5124* (BOL; S).
Cape.—2818 (Warmbad); 5 km E. of Goodhouse (-CD), *Van der Walt 124* (PRE; PRU); 27 km W.N.W. of Pella (-DD), *Van der Walt 119* (PRE: PRU). 2819 (Ariamsvlei): 8 km N.

of Pella (-CC), *Van der Walt 116* (PRE; PRU). 2820 (Kakamas): near Augrabies (-CB), *Pearson 3567* (BOL); near Kakamas (-DC), *Fuller 24* (BOL). 2919 (Pofadder): 6 km N.E. of Pofadder (-AB), *Acocks 21795* (PRE). 2921 (Kenhardt): S. of Kenhardt (-AC), *Hutchinson 952* (BOL).

Several herbarium specimens of *C. oblanceolata* Schinz, among them the type (Dinter 1497), were examined. The male flowers of both *C. gracilifrondosa* and *C. oblanceolata* have 4 stamens. In all descriptions of *Commiphora* species seen so far, the number of stamens was given as 8. It seems likely that the two taxa are closely related. The leaves differ so markedly, however, that they can be considered as two different species, The leaves of *C. oblanceolata* are small (1—1,5 cm long); the petioles seldom exceed a length of 7 mm and the leaflets are oblanceolate with finely serrate margins, which are never lobed.

De Winter who examined the Kew specimens of the two taxa, was convinced that *C. gracilifrondosa* should be considered as a distinct species (letter at Botanical Research Institute, Pretoria). Merxmüller (1970) also recommended that *C. gracilifrondosa* should be described in detail. Dinter's (1928) description of the species is as follows: "Dicht vor Auros sammelte ich auf einem Granit-

FIG. 7.
Commiphora gracilifrondosa.
A–D, leaves.
E, branchlet with leaves and inflorescences.
F, branchlet with leaves and fruits.

blockhügel Zweige einer *Commiphora* mit aussergewöhnlich zierlicher dreizähliger Belaubung und trotz ihres flaschenförmingen holzigsukkulenten Stammes sehr dünnen Endzweigen". A few descriptive words have thus been added, which possibly would facilitate identification of the plant. Therefore, the name cannot be designated as a true "nomen nudum".

It was observed that goats and game graze on the young branches. The local name of "Suikerkan" is probably derived from the sweet taste of the wood.

ACKNOWLEDGMENTS

Thanks are due to Mr. E. G. H. Oliver who compiled the Latin diagnoses, and to Prof. Dr. H. P. van der Schijff for his co-operation in the preparation of the paper. I am also grateful to Prof. Dr. H. Merxmüller and Dr. B. de Winter for their advice. The type specimen of *C. oblanceolata* was kindly lent to me by the Director of the "Botanisches Museum", University of Zürich. The research project was supported by a grant from the C.S.I.R.

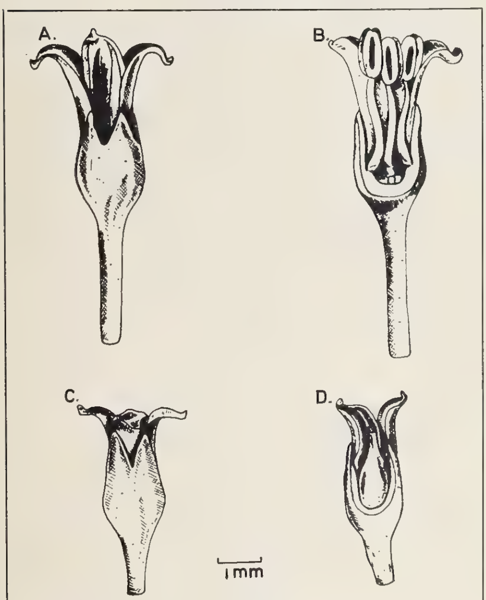

FIG. 8.
Commiphora gracilifrondosa.
A, male flower.
B, longitudinal section of male flower.
C, female flower.
D, longitudinal section of female flower.

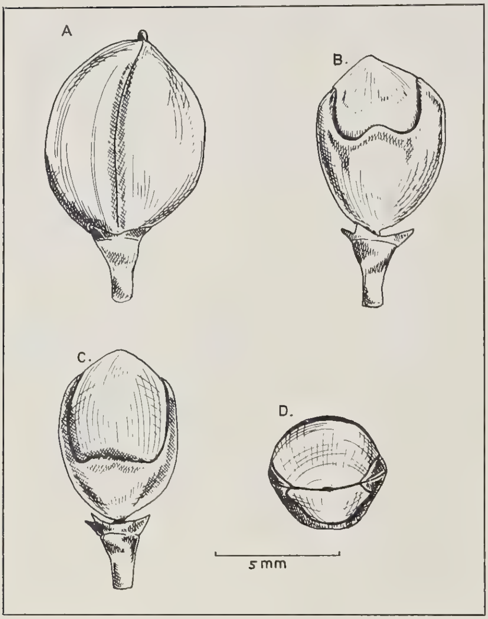

FIG. 9.
Commiphora gracilifrondosa.
A, fruit.
B, deeply convex face of endocarp with pseudaril.
C, shallowly convex face of endocarp with pseudaril.
D, endocarp with pseudaril seen from the apex of endocarp.

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Jl S. Afr. Bot. 37 (3): 199–212 (1971)

FLAVONOIDS OF THE PROTEACEAE, PART 1. A CHEMICAL CONTRIBUTION TO STUDIES ON THE EVOLUTIONARY RELATIONSHIPS IN THE S. AFRICAN PROTEOIDEAE*

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Abstract

The leaves of 103 species of Proteoideae were hydrolysed with hot mineral acid and the hydrolysates were examined by paper chromatography for the presence of chemotaxonomically significant flavonoids. On the hypothesis that the presence of myricetin and leucodelphinidin indicate primitive characters whereas their absence more advanced characters, a scheme representing possible evolutionary relationships within the Proteoideae has been tentatively advanced. The results of this survey also indicate that in the biosynthesis of myricetin in the leaf, leucodelphinidin may be a precursor.

Uittreksel

FLAVONOIDE VAN DIE PROTEACEAE, DEEL 1. 'N CHEMIESE BYDRA TOT DIE STUDIES VAN DIE ONTWIKKELINGS VERWANTSKAPPE IN DIE SUID-AFRIKAANSE PROTEOIDEAE. Die blare van 103 Proteoideae spesies was gehidroliseer met warm mineraal suur en die hidrolisate was ondersoek met papier chromatografie vir die teenwoordigheid van chemotaksonomies belangrike flavonoide. Op die hipotese dat die teenwoordigheid van myricetien en leucodelphinidien, op primitiewe eienskappe aandui en hul afwesigheid, op meer gevorderde eienskappe, 'n raamwerk wat beweer dat daar moontlike evolutionêre verbandskappe in die Proteoideae is word voorlopig geopper. Die resultaat van hierdie ondersoek dui ook daarop aan dat leucodelphinidien die voorloper van die biosintese van myricetien in 'n blaar, mag wees.

Introduction

The family Proteaceae comprising over 1000 species is essentially peculiar to the southern continents (Hutchinson 1959). On morphological grounds it has been subdivided into two sub-families:

(i) the Proteoideae, to which most of the species indigenous to Southern Africa belong, and

(ii) the Grevilleoideae into which most of the Australian species fall.

This paper is concerned with the former subfamily, many of which are to be found in the Western Cape region. It was considered that a study of the flavonoid constituents of the Proteaceae could prove fruitful because the bark of many species was used for tanning purposes during the early Cape days

(*This paper was presented in part at a meeting of the Experimental Biology Group, Mowbray, Cape, on 31st October, 1970.)

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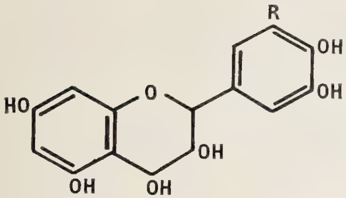
(Watt and Breyer-Brandwijk, 1962). Reviews on the flavonoid chemistry of the Proteaceae by Watt and Breyer-Brandwijk and by Hegnauer (1969) indicate that the coverage to date has been superficial. The most important contribution is the chemotaxonomic survey of eight species by Bate-Smith (1962) and a further thirty species by Van Oudsthoorn (1963). These workers subjected leaves of selected species to hot acid hydrolysis and then used paper chromatography to identify flavonoids and other plant phenolics in each resulting hydrolysate.

The usefulness of flavonoids as taxonomic guides has been discussed by Bate-Smith (1963). The results of his survey on the phenolic constituents in eight hundred species of dicotyledons (Bate-Smith 1962) following on an earlier study (Bate-Smith 1957) led Bate-Smith to conclude that the presence of leucoanthocyanins, as indicated by the production of red colours upon acid hydrolysis, and the presence of compounds having three vicinal hydroxy groups on a benzene ring as found, for example, in leucodelphinidin **2** and myricetin **5**, are both primitive characters, and that the loss of the genes responsible for the biosynthesis of these compounds in the evolutionary line is apparently an irreversible process (Bate-Smith 1962).

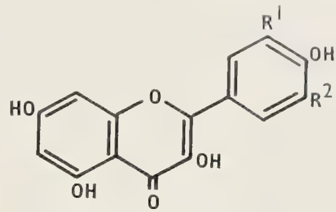
It would appear that Bate-Smith's deductions could be applied to determining evolutionary trends within a given plant family and so complement the work of morphologists and geneticists. A scheme representing the possible evolution of the Proteoideae has for example been advanced by Johnson and Briggs (1963), based upon chromosomal studies. We felt that an extension of the survey of Van Oudtshoorn to include as many of the local Proteaceae as possible might shed additional light on this subject. Van Oudtshoorn himself, in observing myricetin to be present only in the genera *Leucospermum* and *Leucadendron* but not in *Aulax*, *Mimetes*, *Paranomus* and *Protea*, has already commented on the potential of this flavonol for infrafamiliar taxonomic purposes. It was therefore decided to examine other species within the genera already examined as well as other genera such as *Diastella*, *Serruria*, *Sorocephalus* and *Spatalla* which have not been studied. It was further decided at this stage to restrict the study to the determination of the presence or absence of the chemotaxonomically significant flavonoids, *viz*. the leucocompounds leucocyanidin **1** and leucodelphinidin **2**, and the flavonols kaempferol **3**, quercetin **4** and myricetin **5**.

The presence of the leuco-compounds **1** and **2** is shown by the appearance of their respective pigments cyanidin **6** and delphinidin **7**, both formed as a result of oxidation of the leuco-compounds on heating in the presence of mineral acid (Bate-Smith 1962). This same treatment hydrolyses the glycosides of the flavonols **3**, **4** and **5** if these be present in the original material.



1 (R = H), LEUCOCYANIDIN

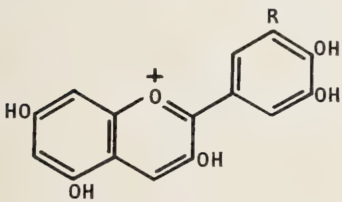
2 (R = OH), LEUCODELPHINIDIN



3 ($R^1 = R^2$ = H), KAEMPFEROL

4 (R^1 = H; R^2 = OH), QUERCETIN

5 ($R^1 = R^2$ = OH), MYRICETIN



6 (R = H), CYANIDIN

7 (R = OH), DELPHINIDIN

Methods and Results

Except where indicated, leaves were collected from labelled plants growing in the National Botanic Gardens, Kirstenbosch, Cape. The freshly-picked leaves were dried in an air oven at 60°C for 24 hours. Chlorophyll and waxes were removed first by subjecting a macerated sample (*ca.* 2 g) for 1–3 hour extraction by light boiling petroleum (b.p. 40–60°C) in a Soxhlet extractor. The sample was then covered with 3 *M* hydrochloric acid (20 ml) in a boiling tube which was immersed in a boiling water bath for 20 to 30 minutes. The hydrolysate was cooled, extracted first with diethyl ether (AnalaR grade, 3×15 ml) to extract the flavones and other phenolics, then with 1-pentanol (2–3 ml) to extract the anthocyanidins. The ethereal extract was washed with water (3 ml) to remove residual acid, then dried over anhydrous sodium sulphate (5 g). The filtered extract was then concentrated to low volume (*ca.* 0,5 ml) for chromatographic examination.

The ether extracts were spotted onto strips of previously washed Whatman paper No. 1, together with myricetin and quercetin as markers. One strip was developed in the Forestal solvent (acetic acid- concentrated hydrocholoric acid-water, 30:3:10) and the other in 60% acetic acid. Descending chromatography was used in all cases. When the solvent had moved 25 cm the chromatograms were dried and examined under ultraviolet light before and after exposure to ammonia vapour. Except where "streaking" occurred, myricetin and quercetin

were easily identified. Kaempferol was identified by its R_f values, 0,56 (Forestal) and 0,46 (60% acetic acid), and its yellow fluorescence under UV light. It was further confirmed by applying the extract to a strip of Whatman No. 1 paper as a band. After development in 60% acetic acid, the band at R_f 0·46 was cut out, extracted into spectroscopically pure ethanol and the spectrum was recorded on a self-recording Beckmann DB spectrophotometer. The absorption band at 368 nm was shifted to 426 nm on addition of aluminium chloride while anhydrous sodium acetate shifted the band at 268 to 275 nm (Jurd, 1962). Other flavonoids and phenolics which were observed on the chromatograms are not reported in this survey.

In a few cases where streaking tended to mask the presence of the flavonols, thin layer chromatography was applied. The ether extracts were spotted onto aluminium sheets coated with polyamide F_{254} (Merck precoated) together with the marker flavonols, and the plates were developed in a methanol-acetic acid-water solvent (90:5:5) (Mabry, Markham and Thomas, 1970). After drying the plates were examined under both 240 and 340 nm lights.

The colour of the 1-pentanol extract with the pigments varied from pink to red-brown. The presence or absence of leucoanthocyanins was estimated visually from the intensity of the colour of this extract. The extracts were then applied to previously washed Whatman No. 1 filter paper strips and, together with cyanidin and delphinidin as markers, using descending technique, one strip was developed in the Forestal solvent (above) and the other in the "Roux" solvent, 90% formic acid- 3 *M* hydrochloric acid (1:1) (Roux, 1957). The chromatograms were dried when the solvent front had moved 25 cm and were examined under UV light. With the prior removal of flavones and other phenolic compounds in the ether extract, both cyanidin and delphinidin were readily identified except where streaking occurred. When these pigments occurred together in the same hydrolysate their relative proportions were estimated approximately by visual comparison of the intensities of the spots on the dry paper chromatograms.

The detailed results of this study on one hundred and three species are reported in Table I.

Since Van Oudtshoorn (1963) had worked on preserved herbarium specimens, we decided to re-examine those species which were available in the Gardens and which he had examined. The names of several species had changed since his study and more especially we wished to assess the relative proportions of cyanidin and delphinidin in the hydrolysates. Where our results appeared to differ from those of Van Oudtshoorn, we have reported our own. Thus Van Oudtshoorn reported myricetin to be present in *Leucadendron ramosissimum* whereas we found this flavonol to be absent from *L. conicum* (= *L. ramosissimum*). We also report the presence of both myricetin and leucodelphinidin in *L. galpinii* whereas

TABLE I

Distribution of Chemotaxonomically-significant Flavonoids among some South African Proteoideae[a]

Species[b]	L-A	D	C	M	Q	K
Aulax cancellata (L.) Druce (=*A. pinifolia* Berg.)	+++	++	(+)	—	+	+
A. pallasia Stapf[c]	+++	++	(+)	?	(+)	?
A. umbellata (Thunb.) R.Br. (=*A. cneorifolia* Salisb. ex Knight[c])	++	+	(+)	—	++	++
Brabeium stellatifolium L.[d]	—	—	—	—	—	—
Diastella bryifloria Salisb. ex Knight[e]	+++	?	+	?	+	?
Faurea macnaughtonii Phill.	+	?	?	—	(+)	?
Leucadendron album (Thunb.) Fourcade	+++	—	+	—	+	(+)
L. argenteum (L.) R. Br.	++	+	—	—	+	(+)
L. conicum (Lam.) Williams (=*L. ramosissimum* Buek and Meisn.)[c]	+++	++	(+)	?	++	(+)
L. cryptocephalum Guthrie	+++	++	(+)	++	++	++
L. daphnoides (Thunb.) Meisn.	+++	—	+	—	++	++
L. discolor Beuk ex Phill. and Hutch.	+++	++	(+)	(+)	+	+
L. galpinii Phill. and Hutch.[c]	+++	++	++	+	+	?
L. gandogeri Schinz ex Gandoger (*L. guthrieae* Salter)	+++	++	(+)	++	+	++
L. globularia (Lam.) Williams	++	++	+	?	(+)	(+)
L. lanigerum Meisn.	+++	++	(+)	—	+	+
L. laureoleum (Lam.) Williams	+++	+	(+)	+	+	+
L. longmorense Williams	+++	++	(+)	—	+	++
L. loranthifolium (Salisb. ex Knight) Williams	+++	—	+	—	(+)	++
L. meyerianum Buek ex Phill. and Hutch.	+++	—	++	—	+	++
L. modestum Williams	+++	++	+	—	+	+
L. muirii Phill.	+++	?	++	—	++	—
L. nobile Williams	++	—	++	—	++	+
L. rubrum Burm. f.	+++	++	(+)	+	++	+
L. sabulosum Salter	+++	++	(+)	—	?	+
L. salicifolium (Salisb.) Williams	+++	++	(+)	(+)	++	+
L. salignum Berg. (=*L. adscendens* R. Br.[c])	+++	++	(+)	+	++	++
L. sessile R. Br.	+++	?	++	++	++	?
L. stellare Sims	+++	++	(+)	+	+	++
L. tinctum Williams	+++	?	+	++	++	?
L. tortum R. Br.	+++	+	+	?	+	++
L. uliginosum R. Br.	+++	++	+	+	++	?
L. xanthoconus (O. Kuntze) K. Schum. (= *L. salignum* R. Br.[c])	+++	++	(+)	++	++	?
Leucospermum bolusii Gandoger	+++	++	(+)	+	++	++
L. catherinae Compton	+++	++	(+)	(+)	+	++
L. conocarpodendron (L.) Buek	+++	+	—	—	?	+
L. cordifolium (Salisb. ex Knight) Fourcade	+++	+	—	+	+	+
L. cuneiforme (Burm. f.) Rourke (= *L. attenuatum* R. Br.)	+++	++	(+)	?	++	++
L. lineare R. Br.[c]	+++	++	(+)	?	+	++
Leucospermum muirii Phill.	+++	++	+	?	++	++
L. patersonii Phill.	+++	++	(+)	+	+	(+)
L. prostratum (Thunb.) Stapf[c]	+++	++	+	+	+	+
L. reflexum Buek ex Meisn.	+++	++	(+)	+	+	+

TABLE I *(continued)*

Distribution of Chemotaxonomically-significant Flavonoids among some South African Proteoideae[a]

Species[b]	L-A	D	C	M	Q	K
L. rodolentum (Salisb. ex Knight) Rourke	+++	++	(+)	++	+	+
L. tottum (L.) R. Br.	+++	++	(+)	?	(+)	+
L. truncatulum (Salisb. ex Knight) Rourke	++	++	(+)	+	+	(+)
L. vestitum (Lam.) Rourke	+++	++	(+)	?	+	++
Mimetes cucullatus (L.) R. Br. (= *M. lyrigera* Salisb. ex Knight[c])	+++	—	++	—	+	(+)
M. fimbriaefolius Salisb. ex Knight	+++	—	(+)	—	+	—
M. hottentoticus Phill.[c]	+++	—	+	—	+	+
Orothamnus zeyheri Hook. f.[f]	+++	—	++	+	+	?
Paranomus reflexus (Phill. and Hutch.) N. E. Br.	+++	+	(+)	—	(+)	+
P. spicatus (Berg.) R. Br.[c]	++	(+)	—	?	+	++
Protea acaulis (L.) Reich	++	?	?	?	?	?
P. acerosa R. Br.	+	?	?	?	?	?
P. amplexicaulis (Salisb.) R. Br.	++	?	?	?	+	?
P. angustata R. Br.	+	?	?	—	?	—
P. arborea Houtt (= *P. grandiflora* Thunb.)	++	—	—	—	?	?
P. aristata Phill.	—	?	?	?	?	?
P. barbigera Meisn.	++	—	(+)	—	+	(+)
Protea canaliculata Haw	++	—	?	—	(+)	?
P. cedromontana Schlechter	++	—	—	—	++	++
P. compacta R. Br.	++	?	(+)	—	++	?
P. cordata Thunb.	++	—	—	?	?	?
P. cynaroides (L.) L.[g]	+	—	—	—	(+)	—
P. decurrens Phill.	++	—	—	—	+	+
P. eximia (Salisb. ex Knight) Fourcade	+	—	—	?	(+)	?
P. glabra Thunb.	+	?	?	?	?	?
P. grandiceps Tratt.	—	?	?	?	?	?
P. harmeri Phill.	+++	—	++	—	++	++
P. lanceolata E. Mey. ex Meisn.	(+)	—	—	—	?	?
P. laurifolia Thunb.[c] (= *P. marginata* Thunb.[c])	+++	?	+	—	++	?
P. longiflora Lam.	+	?	?	?	?	?
P. longifolia Andr.	—	?	?	?	?	+
P. lorifolia (Salisb. ex Knight) Fourcade	++	—	+	—	++	(+)
P. macrocephala Thunb. (= *P. incompta* R. Br.[c])	++	?	?	—	+	?
P. minor Compton	+	?	?	—	?	+
P. mundii Klotzsch[c]	+	?	?	—	?	?
P. nana (Berg.) Thunb.	++	?	?	—	+	?
P. neriifolia R. Br.[c]	+	—	(+)	—	?	+
P. obtusifolia Buek ex Meisn.	+	?	?	—	—	—
Protea odorata Thunb.	++	?	?	—	+	+
P. pityphylla Phill.	+++	—	(+)	—	+	—
P. pulchra Rycroft	++	—	—	—	++	+
P. repens L. (= *P. mellifera* Thunb.)	—	—	—	—	+	?
P. restionifolia (Salisb. ex Knight) Rycroft	+++	—	+	—	+	+
P. rouppelliae Meisn.	+++	—	++	—	+	(+)
P. rubropilosa Beard	++	—	—	—	?	—

TABLE I (*continued*)

Distribution of Chemotaxonomically-significant Flavonoids among some South African Proteoideae[a]

Species[b]	L-A	D	C	M	Q	K
P. rupicola Meisn.	+	—	—	—	?	?
P. scabra R. Br.	+++	—	(+)	?	+	?
P. scolymocephala (L.) Reich.	+	?	?	?	?	?
P. simplex Phill.[c,h]	++	?	+	?	(+)	?
P. speciosa (L.) L.	++	?	+	—	+	(+)
P. stokoei Phill.	+	?	?	—	?	?
P. sulphurea Phill	++	?	?	—	(+)	—
P. venusta Compton	++	?	?	—	+	(+)
P. welwitschii Engl.[i] (= *P. hirta* Klotzsch[e])	+++	++	+	—	+	(+)
P. witzenbergiana Phill.	++	?	+	—	+	(+)
Serruria adscendens R. Br.	+++	+	+	++	++	++
S. aemula R. Br.	++	++	+	++	?	?
S. barbigera Salisb. ex Knight	+++	++	+	+	+	(+)
S. florida (Thunb.) Salisb. ex Knight	++	++	(+)	++	++	?
Serruria pedunculata (Lam.) R. Br. (= *S. artemesiaefolia* Salisb. ex Knight)	+++	++	+	?	+	+
Sorocephalus lanatus (Thunb.) R. Br.[j]	+++	++	(+)	?	+	+
Spatalla curvifolia Salisb. ex Knight	++	+	+	—	+	+
S. incurva (Thunb.) R. Br.[k]	+++	++	(+)	+	+	?

Footnotes to Table I.

[a] The abbreviations are as follows: L–A = leucoanthocyanin reaction, with D and C = delphinidin and cyanidin respectively, each formed from a leucocompound; M = myricetin; Q = quercetin; K = kaempferol. The symbols +++, ++, +, (+) and — refer to the relative strength or absence of the particular constituent in question. Where there is doubt about the presence of a constituent, either because of its low concentration or because it is masked by some trailing contaminant or by heavy concentration of a neighbouring constituent, it is indicated by '?'.

[b] Except where indicated below, all material was collected from labelled plants growing in the National Botanic Gardens, Kirstenbosch, Cape (NBG-K).

[c] This species has been examined by Van Oudtshoorn.

[d] This species belongs to the Grevilleoideae.

[e] Herbarium collection of J. P. Rourke, JPR 920.

[f] Herbarium collection, NBG-K 87352.

[g] This species has been examined by Bate-Smith (1962).

[h] Herbarium collection, NBG-K 1768.

[i] Herbarium collection, NBG-K 1445.

[j] Herbarium collection, NBG-K 85734.

[k] Herbarium collection, JPR 25.

these compounds were reported to be absent. In *Mimetes* the former *M. lyrigera* was reported to give a doubtful positive leucoanthocyanin reaction with cyanidin absent. For *M. cucullatus* (= *M. lyrigera*) we obtained a strong leucoanthocyanin reaction and observed cyanidin in the hydrolysate. There also appears to be some confusion over *Protea laurifolia* (= *P. marginata*). *P. laurifolia* is reported to give positive tests for both leucocyanidin and leucodelphinidin whereas *P. marginata* gave a doubtful test for the latter and no leucocyanidin. We obtained cyanidin but no delphinidin from fresh leaves of *P. laurifolia*. We have also obtained cyanidin but not delphinidin from a preserved specimen of *P. simplex*. The same herbarium specimen was previously reported to give both these anthocyanidins.

A general survey of the results in Table I leads to some interesting conclusions:

(1) Except in the case of the rare species, *Orothamnus zeyheri*, leucodelphinidin is always present when myricetin occurs. The leuco-compound **2** however frequently occurs without myricetin. A close study of the results of Bate-Smith (1962) appears to support this observation with but few exceptions. If one accepts the hypothesis that delphinidin and myricetin are formed in the plant from the same 3′, 4′, 5′-trihydroxy-precursor (Harborne, 1962), one is led to conclude that leucodelphinidin is possibly the precursor of myricetin.

It should be stressed at this point that the absence of leucodelphinidin in the leaf does not necessarily mean its total absence from the plant. For example we have observed delphinidin to be present in the hydrolysate of the bracts of *Protea macrocephala* but the leaves gave only a moderate leucoanthocyanin reaction while the presence of both cyanidin and delphinidin in the hydrolysate was questionable. It would appear therefore that genetic control in the synthesis of flavonoids in the leaf is independent of that in the bracts.

(2) Leucodelphinidin is peculiar not only to the genera *Leucospermum* and *Leucadendron* as observed by Van Oudtshoorn but is also found in the minor genera *Aulax*, *Paranomus*, *Serruria*, *Sorocephalus* and *Spatalla*. Since leucoanthocyanins condense to form tannins (Bate-Smith and Metcalfe, 1957), it is not surprising that the barks of many *Leucospermum* and *Leucadendron* spp were once widely used in tanning (Watt and Breyer-Brandwijk, 1962).

(3) Most *Protea* spp give either weak or negative leucoanthocyanin reactions and myricetin was absent in all forty-three species examined.

(4) Of the flavonoids considered, there appears to be little or no correlation between the presence or absence of kaempferol and the other flavonoids.

TABLE II.

GROUP I:	L-A (+++); M (+); D (++); C (±); Q (+); K (±).
Leucadendron:	*L. cinerum*[a]; *L. corymbosum*[a]; *L. cryptocephalum: L. discolor; L. eucalyptifolium*[a]; *L. galpinii; L. gandogeri* (= *L. guthrieae*); *L. glabrum*[a]; *L. laureoleum; L. rubrum; L. salicifolium; L. salignum* Berg (= *L. adscendens*[a]); *L. sessile; L. stellare; L. tinctum; L. uliginosum; L. xanthoconus* (= *L. salignum* R. Br.[a])
Leucospermum:	*L. bolusii; L. buxifolium*[a]; *L. catherinae: L. cordifolium; L. patersonii; L. prostratum; L. reflexum; L. rodolentum; L. tomentosum*[a]; *L. truncatulum.*
Orothamnus:	*O. zeyheri*[b].
Serruria:	*S. adscendens; S. aemula*[c]; *S. barbigera; S. florida.*
Spatalla:	*S. incurva.*
GROUP II:	L-A (+++); M (—); D (+); C (+); Q (+); K (+).
Aulax:	*A. cancellata* (= *A. pinifolia*); *A. pallasia*[a]; *A. umbellata* (= *A. cneorifolia*[a])
Leucadendron:	*L. argenteum; L. conicum* (=*L.ramosissimuma*); *L. globularia; L. lanigerum; L. longmorense: L. modestum; L. sabulosum*[c]; *L. tortum.*
Leucospermum:	*L. conocarpodendron*[c]; *L. cuneiforme;* (= *L. attentuatum*[a,c]) *L. lineare; L. muirii; L. tottum; L. vestitum.*
Paranomus:	*P. medius*[a]; *P. reflexus; P. spicatus.*
Protea:	*P. welwitschii* (= *P. hirta*[a])
Serruria:	*S. pedunculata* (= *S. artemesiaefolia*).
Sorocephalus:	*S. lanatus.*
Spatalla:	*S. curvifolia.*
GROUP III:	L-A (+++); M (—); D (—); C (+); Q (+); K (±).
Diastella:	*D. bryiflora.*
Leucadendron:	*L. abietinum*[a]; *L. aemulum*[a]; *L. album; L. crassifolium*[a]; *L. daphnoides; L. loranthifolium; L. meyerianum; L. muirii; L. nobile.*
Mimetes:	*M. cucullatus* (= *M. lyrigera*[a]); *M. fimbriaefolius; M. hottentoticus.*
Protea:	*P. barbigera; P. compacta; P. harmeri; P. laurifolia* (= *P. marginata*[a]); *P. lorifolia; P. neriifolia*[c]; *P. pityphylla; P. restionifolia; P. rouppelliae; P. scabra; P. simplex; P. speciosa; P. witzenbergiana.*
GROUP IV:	L-A (++ to —); M (—); D (—); C (—); Q (±); K (±).
Faurea:	*F. macnaughtonii.*
Protea:	*P. acaulis; P. acerosa; P. amplexicaulis; P. angustata; P. arborea; P. aristata; P. canaliculata; P. cedromontana; P. cordata; P. cynaroides; P. decurrens; P. eximia; P. glabra; P. grandiceps; P. lanceolata; P. longiflora; P. longifolia; P. macrocephala* (= *P. incompta*[a]); *P. minor; P. mundii; P. nana; P. obtusifolia; P. odorata; P. pulchra; P. repens; P. rubropilosa; P. rupicola; P. scolymocephala; P. stokoei; P. sulphurea; P. venusta.*

Footnotes to Table II.

[a] Result from Van Oudtshoorn's paper.

Delphinidin absent.

[c] Quercetin ? or —.

DISCUSSION

In Table II an attempt to correlate the data presented in Table I has been made. Consequential to the Bate-Smith hypothesis, a grouping of the genera of the Proteoideae based on the flavonoids present was first considered. However, since it was apparent that within each genus specific variations do occur, it was

thought to be more appropriate to group the different species as shown in Table II. Four groups in increasing order of evolutionary advancement become apparent. In order to add weight to the significance of the correlations, the results of Bate-Smith (1962) and Van Oudtshoorn (1963) have been included in the groups.

GROUP I: This comprises those species giving an intense leucoanthocyanin reaction and contain both leucodelphinidin and myricetin. They may thus be regarded as the most primitive species of the Proteoideae living. Leucocyanidin is either absent or only present in low concentration. Quercetin is present in all but one species. The group is dominated by 17 *Leucadendron* spp and 10 *Leucospermum* spp. Four of the five *Serruria* spp examined and one *Spatalla* also belong. Although *Orothamnus zeyheri* gave a negative leucodelphinidin reaction, it has been included with this group as it contains myricetin.

GROUP II: The species here again all give intense leucoanthocyanin reaction but myricetin was not detected. They are therefore more advanced than those in Group I. Leucocyanidin is present in amounts approximately equal to leucodelphinidin and quercetin is present in all but four of the species examined. Eight of the twelve genera examined are represented in this group which is dominated by 8 *Leucadendron* spp and 6 *Leucospermum* spp. The 3 *Aulax* spp and 3 *Paranomus* spp examined all belong to this group as well as one species each of *Serruria*, *Sorocephalus* and *Spatalla*. It is interesting to observe that of the 45 species of *Protea* examined, only *P. welwitschii* falls into this group.

GROUP III: Those species giving a moderate to strong leucoanthocyanin reaction and containing leucocyanidin but neither myricetin nor leucodelphinidin are assigned to this group. Quercetin was present in all but one species. Group III is dominated by 9 *Leucadendron* spp and 13 *Protea* spp. The three *Mimetes* spp examined as well as *Diastella bryiflora* all fall into this group.

GROUP IV: The species in this group gave only a weak to negative leucoanthocyanin reaction. Both leucocyanidin and leucodelphinidin were either absent or, if present, in a concentration too low for detection. Quercetin may or may not be present. The group is largely dominated by 31 *Protea* spp with *Faurea macnaughtonii*, the only other species belonging.

Brabeium stellatifolium, the only indigenous species of the Grevilleoideae, was also examined. It may be described as a Group IV type.

The significance of the data as correlated in Table II becomes clearer when summarised as in Table III. Potential evolutionary trends become apparent as determined solely by the flavonoid constituents and it would appear that the evolutionary line within a given genus does follow the sequence as suggested earlier, thus:

GROUP I $\rightarrow$ GROUP II $\rightarrow$ GROUP III $\rightarrow$ GROUP IV.

TABLE III

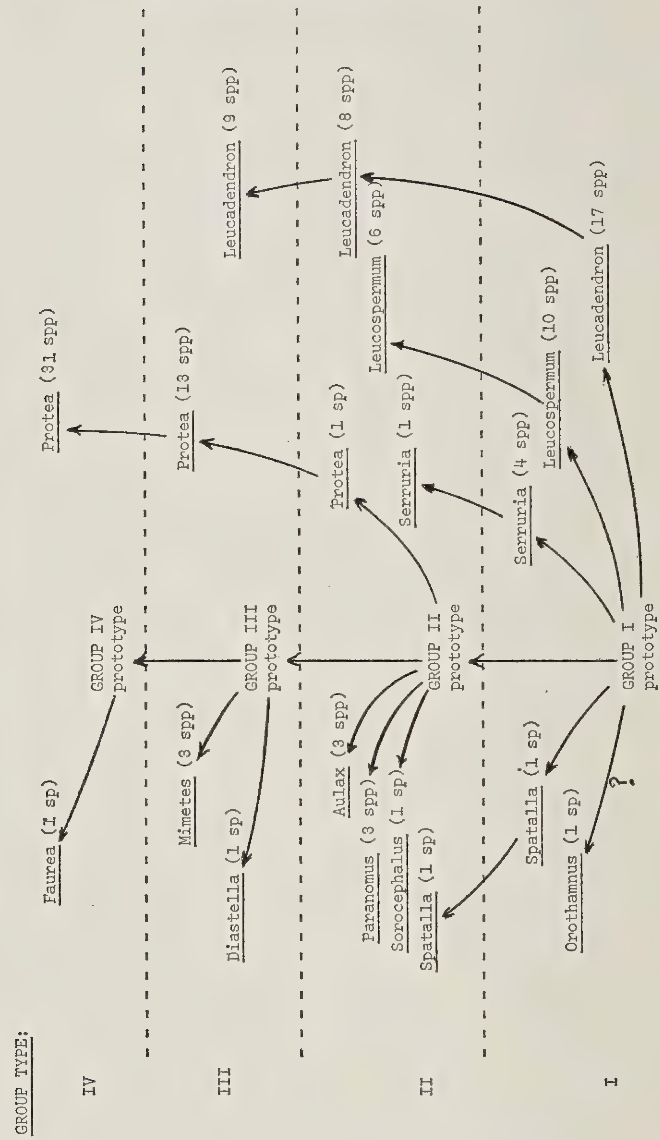
	GROUP I	*GROUP II*	*GROUP III*	*GROUP IV*	*No. of Species*
L-A	+++	+++	+++	++ to —	
M	+	—	—	—	
D	+	+	—	—	
C	±	+	+	—	
Q	+	+	+	±	
K	±	±	±	±	
GENUS:					
Aulax	0	3	0	0	3
Diastella	0	0	1	0	1
Faurea	0	0	0	1	1
Leucadendron	17	8	9	0	34
Leucospermum	10	6	0	0	16
Mimetes	0	0	3	0	3
Orothamnus	1	0	0	0	1
Paranomus	0	3	0	0	3
Protea	0	1	13	31	45
Serruria	4	1	0	0	5
Sorocephalus	0	1	0	0	1
Spatalla	1	1	0	0	2

Consequently when a Group I species loses genetic control over the oxidation of leucodelphinidin (or the appropriate trihydroxy precursor) to myricetin it becomes a Group II species. Similarly a Group II species on losing genetic control over the synthesis of leucodelphinidin becomes a Group III species, and this in turn becomes a Group IV species when it fails to synthesise leucocyanidin. These deductions indicate that in the leaf the origins of the flavonols myricetin and quercetin are not necessarily parallel as suggested by Harborne (1962). The evidence from our studies strongly suggests that leucodelphinidin is the precursor of myricetin but leucocyanidin cannot be the precursor of quercetin since this flavonol is often found when this leuco-compound is absent.

A possible mode of the evolution of the Proteoideae as determined by the presence or absence of chemotaxonomically significant flavonoids is presented in the figure. It is suggested that the earliest species within a genus arose from a prototype having essentially the same leaf flavonoids. Clearly one prototype can, by losing genetic control over the synthesis of one of these flavonoids, give rise to a more advanced prototype. For clarity each prototype and those species belonging to the same flavonoid group have been separated from dissimilar ones by horizontal lines.

Since only about one quarter of all the Proteoideae have been examined, the scheme can only be regarded as being very tentative at this stage. For a more precise assessment of the prototype giving rise to a particular genus, the whole field of the Proteoideae requires study. One may then find that the smaller

FIGURE: POSSIBLE EVOLUTIONARY SEQUENCES WITHIN THE PROTEOIDEAE



species which have apparently arisen from the prototypes of Group II and III have their origin in the Group I prototype. This may be the explanation of the apparent disparity between *Orothamnus* and *Mimetes*, two morphologically related genera (Johnson and Briggs, 1962). It is therefore necessary to study other *Mimetes* spp to determine possible earlier origins. There is also the possibility that a more primitive species of a genus has become extinct, a hypothesis which cannot be tested but nevertheless cannot be excluded. Such a possibility may apply not only to the genus *Mimetes* but to all the other genera studied. Were this in fact to be true, no definite conclusions can be drawn as to common origins of present living genera, as based solely on the presence or absence of the significant leaf flavonoids. However, the method of testing for these leaf flavonoids is not without merit for it clearly demonstrates the degree of evolutionary development within a given genus. For example it would appear, from present results, that *Serruria* and *Leucospermum* have not advanced as far as *Leucadendron* while *Protea*, arising apparently from a Group II prototype, has advanced most of all.

In concluding this discussion, the results pose a number of interesting questions:

(1) How do leaf flavonoids change as a result of hybridisation, particularly when species of different groups are crossed?

(2) Does a change in the leaf flavonoids in a given species indicate a new species or a subspecies? The answer to this question may lead to a remodelling of the larger genera, particularly *Protea* as delimited at present in "Flora Capensis" (Thiselton-Dyer *et al.*, 1912).

The urge to discover the answers to these and other questions justifies extending this survey to include as many as possible, if not all, of the Proteoideae.

ACKNOWLEDGMENTS

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AN ECOLOGICAL SURVEY OF THE GRASSLANDS OF THE NGOYE FOREST RESERVE, ZULULAND

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ABSTRACT

A brief quantitative account of the grassland of the Ngoye Forest Reserve is given.

UITTREKSEL

'N EKOLOGIESE OORSIG VAN DIE GRASLANDE VAN DIE NGOYE WOUD-RESERVAAT, ZULULAND.

'n Beknopte kwantitatiewe verslag van die grasveld van die Ngoye Woudreservaat word aangebied.

INTRODUCTION

The Ngoye Forest Reserve is situated in Bantu Reserve No. 9 in the Mtunzini District of Zululand. A road via the Amanzanyama School makes entrance into the eastern part of the Reserve possible. The western section is almost inaccessible, even for four-wheel-drive vehicles, because of the exceedingly poor condition of the track leading through very rugged terrain via Obanjeni and Engonyameni to this part of the Reserve.

ENVIRONMENTAL FACTORS

The topography, geology, climatic and other physical factors are discussed by Huntley (1965) and are thus omitted from this paper.

THE GRASSLAND

The Reserve is 2 906,3 ha of which approximately 1 000 ha is grassland (Huntley, 1965). About one third of the grassland is found in the eastern part of the Reserve, while a large portion of the remainder covers the western ridges (Fig. 1).

The eastern grassland covers an area of low hills that range in altitude from 200—300 m. The western grassland, extending from 360—450 m in altitude, is found on very rugged terrain of high, steep ridges and deep narrow ravines. The slopes of these ridges are covered by grass, while below the grassland the bottoms of the ravines are clothed in dense forest.

Method of Survey: On a map of the Reserve the grassland areas were

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divided in squares of equal size. Each square was numbered and equally numbered slips of paper drawn from a "hat" indicated the random localities of the survey,

The wheel-point method of survey (Tidmarsh & Havenga, 1955) was used. A total of 1 500 points was made in each of the grassland areas. The survey, which took place in March, was carried out to determine the floristic composition and basal cover of the grasslands of the Reserve.

Instead of the double-wheel, steel apparatus used by Tidmarsh & Havenga (1955) a single-wheel apparatus of aluminium, developed by the late von Broembsen of the Institute for Botanical Research, Pretoria, was used. The von Broembsen apparatus is much lighter, smaller to transport and easier to handle in rugged terrain.

The criteria for strikes and misses defined by Tidmarsh & Havenga (1955) were applied.

The results of this survey are listed in Tables 1 and 2.

Discussion

The Eastern Grassland. This area has a total basal cover of 35,49 percent (Table 1), which is high but normal for a region of high rainfall (Killick, 1963; Venter, 1969; & West, 1951).

Paspalum commersonii and *Hyparrhenia filipendula* are the two dominants, with true basal covers of respectively 5,86 and 5,06 percent (Table 1). Their relative basal covers are respectively 16,5 and 14,3 percent (Table 1). The subdominant species are *Tristachya hispida*, *Setaria sphacelata*, *Centella coriacea*, *Eragrostis capensis*, *Bulbostylis contecta*, *Digitaria macroglossa* and *Sporobolus centrifugus* of which the true basal covers vary from 1,86 to 3,53 percent (Table 1). It is of interest to note that *Centella coriacea*, a forb, attains such an important position in this grassland.

It was observed during various visits to the Reserve that *Lasiosiphon splendens*, *Arthrosolen calcephalus*, *Helichrysum adscendens*, *H. appendiculatum*, *Aspilia natalensis* and *Pseudarthria hookeri* are typical aspect dominants when in full bloom.

The Western Grassland. The total basal cover amounts to 28,43 percent (Table 2).

Aristida junciformis is completely dominant with a basal cover of 12,26 percent and relative basal cover of 43,1 percent (Table 2). The three subdominants, *Paspalum commersonii*, *Eragrostis capensis* and *Hyparrhenia filipendula* have much lower true basal cover values of respectively 3,20, 3,00 and 2,86 percent. The majority of the species struck, have basal values of less than 1 percent.

A typical aspect dominant on burnt patches is *Senecio latifolius*.

The grassland form of *Stangeria eriopus* is common in this area and seems to be unaffected by the frequent fires that occur in this grassland.

From the survey of the two areas it becomes evident that the vegetation of the eastern grassland has more valuable grazing grasses present as dominants, with a true basal cover of 7,06 percent higher than that of the western grassland. *Aristida junciformis*, the western dominant species, has no grazing value except in the very young stage and hence the frequent burning of the *Aristida* grassveld to provide new grazing. *A. junciformis* has a relative basal cover of 0,4 percent in the eastern grassland (Table 1) compared to 43,1 percent relative cover value in the western grassland (Table 2).

There is a considerable decrease in the number of grass species from the eastern to the western area. A total of 21 species were recorded in the eastern grassland, against 13 species in the western grassland (Tables 1 & 2). Veldmismanagement is most probably the cause of this disappearance of less hardy species of grass.

The Leguminosae reveals a decrease similar to that of the Gramineae.

A comparison of these grasslands of the Ngoye Forest Reserve with the surrounding grasslands reveals the following:

i) The western grassland resembles the grassland of the surrounding Bantu Reserve to a high degree. In both areas *Aristida junciformis* is the exclusive dominant species with high cover values. Venter, (1969) e.g. found basal cover values ranging from 6,9 to 15,1 percent for *A. junciformis* in typical mismanaged grassveld, comparable to the 12,26 percent of the western grassland.

ii) The eastern grassland has dominants which one never finds as dominants in the surrounding Bantu Reserves. These species are, however, important and conspicuous in protected areas such as the Enseleni Nature Garden near Empangeni.

iii) According to Bayer (1938) *Themeda triandra* should be a dominant in the Zululand grasslands. This dominance is clearly demonstrated in the Enseleni Nature Garden where under protection *T. triandra* completely dominates the grassland. The low cover values of this species in the Ngoye Forest Reserve, 0,66 and 0,06 percent (Tables 1 & 2) in the eastern and western parts respectively, suggests that even the eastern grassland is not of the Zululand climax grassland type.

Conclusion

The above survey and comparisons suggest that the grassland of the Ngoye Forest Reserve is in need of proper protection, especially against fires which so frequently spread into the Reserve from the surrounding areas.

TABLE 1

Wheel-point Survey of the *Paspalum/Hyparrhenia* Community
(Summary of the results of 1 500 points)

	True* basal cover	Relative† basal cover
	percentage	
Paspalum commersonii	5·86	16·5
Hyparrhenia filipendula	5·06	14·3
Tristachya hispida	3·53	9·9
Setaria sphacelata	3·06	8·6
Centella coriacea	2·66	7·5
Eragrostis capensis	2·20	6·2
Bulbostylis contecta	2·20	6·2
Digitaria macroglossa	2·13	6·0
Sporobolus centrifugus	1·86	5·2
Trachypogon spicatus	1·00	2·8
Themeda triandra	0·66	1·9
Cyperus obtusiflorus	0·66	1·9
Sporobolus africanus	0·60	1·7
Eulalia villosa	0·60	1·7
Paspalum distichum	0·40	1·1
Coelorhachis capensis	0·33	0·9
Aristea cognata	0·26	0·7
Hyparrhenia cymbaria	0·26	0·7
Scleria melanomphala	0·26	0·7
Desmodium hirtum	0·20	0·6
Eragrostis curvula	0·20	0·6
Argyrolobium rupestre	0·13	0·4
Zornia capensis	0·13	0·4
Hypoxis argentea	0·13	0·4
Aristida junciformis	0·13	0·4
Andropogon shirensis	0·06	0·2
Berkheya setifera	0·06	0·2
Brachiaria brizantha	0·06	0·2
Cassia mimosoides	0·06	0·2
Commelina africana	0·06	0·2
Elyonurus argenteus	0·06	0·2
Panicum maximum	0·06	0·2
Pycreus ferrugineus	0·06	0·2
Stenotaphrum secundatum	0·06	0·2
Syncolostemon argenteus	0·06	0·2
Tephrosia longipes	0·06	0·2
Thesium natalense	0·06	0·2
Unidentified	0·26	0·7
Total	35·49	100·4

* *True basal cover*—Total number of points at which a species was recorded as a percentage of the total number of points made.

† *Relative basal cover*—Total basal cover of one species as a percentage of the total basal cover of all species.

TABLE 2

Wheel-point Survey of the *Aristida/Paspalum* Community
(Summary of the results of 1 500 points)

	True basal cover	Relative basal cover
	percentage	
Aristida junciformis	12·26	43·1
Paspalum commersonii	3·20	11·3
Eragrostis capensis	3·00	10·6
Hyparrhenia filipendula	2·86	10·1
Djigitaria macroglossa	1·66	5·8
Cyperus obtusiflorus	1·60	5·6
Bulbostylis contecta	1·46	5·1
Sporobolus africanus	0·66	2·3
Trachypogon spicatus	0·46	1·6
Tristachya hispida	0·26	0·9
Eulalia villosa	0·13	0·5
Eragrostis curvula	0·13	0·5
Hypoxis argentea	0·13	0·5
Brachiaria humidicola	0·06	0·2
Themeda triandra	0·06	0·2
Sporobolus pyramidalis	0·06	0·2
Senecio erubescens	0·06	0·2
Centella coriacea	0·06	0·2
Aristea cognata	0·06	0·2
Unidentified	0·26	0·9
Total	28·43	100·0

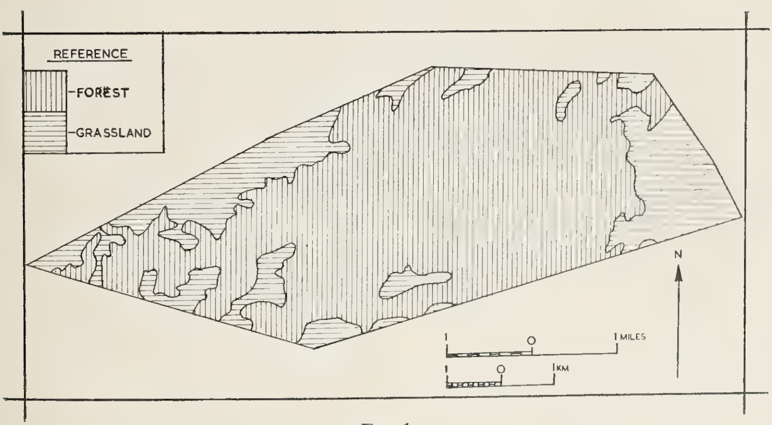

FIG. 1.

Map of the Ngoye Forest Reserve.
(After South Africa 1:50 000 Sheet 2831CC Blackburn)

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iv) Dr. K. Gordon-Gray, University of Natal, for naming the Cyperaceae specimens.

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THE RESPONSE OF *QUERCUS PALUSTRIS* TO ENVIRONMENTAL FACTORS

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Abstract

The diurnal fluctuations in stem diameter and the daily radial growth of *Quercus palustris* growing in the Jonkershoek Forest Reserve were measured with microdendrographs. The data were correlated with meteorological records from an adjacent weather station.

Temperature and difference between precipitation and evapotranspiration appeared as the most influential variables. Independently of the effect of these factors the diurnal fluctuations continued to show short-term cycles within the annual cycle. This indicates that there is an internal control of shrinkage and swelling which is independent of the influence of external factors.

Uittreksel

DIE REAKSIE VAN *QUERCUS PALUSTRIS* OP OMGEWINGSFAKTORE

Die daaglikse wisseling in die deursnee van die stam asook die daaglikse groei van die *Quercus palustris* wat in die Jonkershoekbosreservaat groei, was deurmiddel van mikrodendrograwe gemeet. Die data was gekorreleer met rekords van 'n naburige weerstasie.

Dit het voorgekom asof temperatuur en verskille tussen neerslag en evapotranspirasie die veranderlikes was wat die meeste invloed gehad het. Afgesien van die uitwerking van hierdie faktore het die daaglikse wisseling voortgegaan om kort kringlope binne die jaarlikse kringloop te toon.

Dit dui daarop dat daar 'n inwendige kontrole van die krimp en swelling is wat onafhanklik van die invloede van buite is.

Introduction

It is technically impossible to study the growth behaviour of mature trees under controlled conditions in greenhouses. A study of growth responses under natural conditions therefore may be useful to supplement experiments conducted with seedlings in controlled environments. Not only the influence of single factors, but also the interaction between several environmental factors may change with increasing age of the trees.

In several studies the site indices of stands have been correlated with observed external factors. In South Africa this method has been applied in plantations of black wattle (Schönau 1970). These studies can be useful to guide the forester in selecting species for specific sites, particularly in afforestation with exotics. The site index however, being an index of growth vigour, reflects the cumulative growth from the date of planting up to the present age of the stand but does not account for the year-to-year variations in certain environmental influences. In addition the site index of a stand is affected by management practices and by the

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occurrence of pests and diseases. Finally the method assumes that height growth is indicative for volume growth. Yield studies conducted in Germany however show that the relationship between height and total volume productions is influenced by undisclosed environmental factors, in addition to the widely recognized influence of stand density (Assmann 1961). It is apparent that diameter and height respond differently to the environment.

As an alternative to the site index method, the radial growth of mature trees can be measured over short periods within the growing season and correlated with environmental conditions prevailing during and prior to those periods. These studies afford a better understanding of the progressively changing influence of environmental factors on radial growth. The scope of these investigations is limited because the diameter growth during a given interval does not adequately reflect the total integrated effect of the physical environment.

This paper deals with a growth study conducted during the growing season 1968–1969 on two 25-year old trees of *Quercus palustris* in the Jonkershoek Forest Reserve in the south-western Cape Province. The author gratefully acknowledges permission granted by the Department of Forestry to conduct these studies and to use weather data from the Biesievlei meteorological station operated by the Department.

Quercus palustris is a species which grows under a wide range of conditions in the eastern and central states of North America, between 34° and 42° N latitude and between 70° and 96° W longitude. The mean annual temperature varies between 10° and 16°C and the rainfall between 900 and 1 300 mm per annum. The species grows in pure stands on heavy soils of excessive wetness, and in mixture with hardwoods on lighter and better-drained soils. The trees used in the present study were growing at an altitude of 700 ft/213,41 m above sea level at 33° 55′ E longitude. Microdendrographs, providing a continuous record of the radial growth, were installed at breast height. The growth data were correlated with weather data from the nearest meteorological station Biesievlei, which is situated at an altitude of 950 ft/289,63 m above sea level and at a distance of 1,4 miles/2,25 km from the site of the experimental trees.

The rainfall from 1st April 1968 to 31st March 1969 was 1 438 mm, i.e. 6,1% above the 16-year average for this gauge, as calculated by Wicht (Wicht 1969). Of this total, 74,2% was recorded between April 1 and September 30. Of the summer rainfall, occurring between October 1 and March 31, 36,3% was recorded during October. November was the driest month, with a rainfall of 11 mm. The rain intensity, defined as the average precipitation on rainy days was 13,5 mm during the winter (April 1 to September 30) and 8,4 mm during the summer (October 1 to March 31). The average length of dry spells was 3,6 days

during the winter period and 6,7 days during the summer. During the winter period there were 14 and during the summer period 106 summer days with a maximum temperature > 25°C. The number of tropical days with a maximum temperature > 30°C was 1 during winter and 35 during the summer.

The daily maximum and minimum temperatures were linearly related. An analysis of covariance indicated that the slopes of the regression lines for the previously defined summer- and winter periods did not differ significantly but the difference between the levels was significant at 0,01. The equations were:

$$\text{summer period: } T_{\text{min.}}\ (^\circ C) = 4{,}58 + 0{,}308\ T_{\text{max.}}\ (^\circ C)$$
$$\text{winter period: } T_{\text{min.}}\ (^\circ C) = 1{,}66 + 0{,}308\ T_{\text{max.}}\ (^\circ C)$$

For a 1° increase in the daily maximum temperature the daily minimum temperature increases by 0,31°C. At a given maximum temperature the minimum temperature during the summer period was 3° higher than during the winter period. For the summer period the variance about the regression line was 7,41° and for the winter period this variance was 12,32°. This indicates that the variation around the regression line during the winter was significantly greater than during the summer ($F = 1{,}66$, 181 and 180 degrees of freedom). For a daily maximum temperature of 25°C, the minimum temperature was 12,28°C during the summer period and 9,36°C during the winter period. For a confidence coefficient of 0,95 the confidence interval for a single predicted minimum temperature for $T_{\text{max.}} = 25^\circ$ was $12{,}28 \pm 2{,}73^\circ$ during the summer and $9{,}36^\circ \pm 3{,}53^\circ$ during the winter.

On rainy days during the winter period, temperature and rainfall were significantly related ($r = 0{,}374$, 77 degrees of freedom). The regression equation was:

$$T_{\text{mean}}\ (^\circ C) = 12{,}308 - 0{,}0262\ (\text{rainfall in mm})$$

On rainless days during this period, the mean daily temperature was 13,43°C. During the summer period the mean temperature and rainfall on rainy days were not related ($r = 0{,}241$, 42 degrees of freedom). On rainy days the average mean daily temperature was 16,21°C and on rainless days 19,74°C. The difference between these means was highly significant ($t = 5{,}95$, 178 degrees of freedom).

During the winter period there was a highly significant correlation between hours sunshine and rainfall on rainy days ($r = 0{,}374$, 77 degrees of freedom), the regression equation being as follows:

Hours sunshine: 2,855—0,0526 (rainfall in mm.) On rainless days during this period the average number of hours sunshine was 6,6. During the summer the correlation between hours sunshine and rainfall on rainy days was not

significant ($r = 0,168$, 42 degrees of freedom.) The average number of hours sunshine was 4,43 on rainy days and 8,9 on rainless days.

Procedure and Results

Microdendrographs, providing a continuous record of radial dimensional changes in the diameter of tree trunks were installed on two mature trees of *Q. palustris* at Jonkershoek, at a height of 4,5 ft/1,37 m above ground. The instruments were equipped with 7-day clocks and provided a 1:100 magnification of radial swelling and shrinkage. Daily fluctuation and daily growth, measured on the dendrograph charts were correlated with meteorological data of Biesievlei.

(1) *Diurnal fluctuations.*

Previous studies, conducted in *Pinus radiata* and *Populus deltoides* revealed the occurence of diurnal fluctuations in the diameter of tree trunks (van Laar 1967, 1969). Fluctuations occurring in the xylem and phloem result from absorption lagging behind transpiration, whereas swelling and shrinkage of the bark can be described as a physical evaporation and dehydration process.

During day-time, the rate of transpiration exceeds the rate of water absorption but during the night the position is reversed. For this reason the stem diameter reaches a daily maximum at about 8.00 a.m. and a minimum at 5.00 p.m. For the purpose of this study the daily fluctuation was expressed as the average of the differences between the early-morning maximum and late-afternoon minimum and that between this minimum and the maximum on the next morning. This is an adequate expression for the diurnal fluctuation, although it should be borne in mind that a shower occurring after the afternoon minimum but before 8.00 a.m. on the next day will increase the calculated fluctuation. The readings started on 4th October and were discontinued on 22nd May. After this date no noticeable fluctuations were observed. The annual course of the daily fluctuations, represented as moving averages for 7-day periods is shown in fig. 1. There is a pronounced annual trend which, for the first part of the growing season coincides with the annual growth curve. Within this annual cycle there are clearly distinguishable oscillations of varying lengths. A run-test in which the single observations were classified as above or below the trend, indicated rejection of the hypothesis of randomness at a risk level far below 0,01.

The serial correlation, defined as the correlation between pairs of values of a time series with a fixed distance apart, has been calculated for lags up to 7 days.

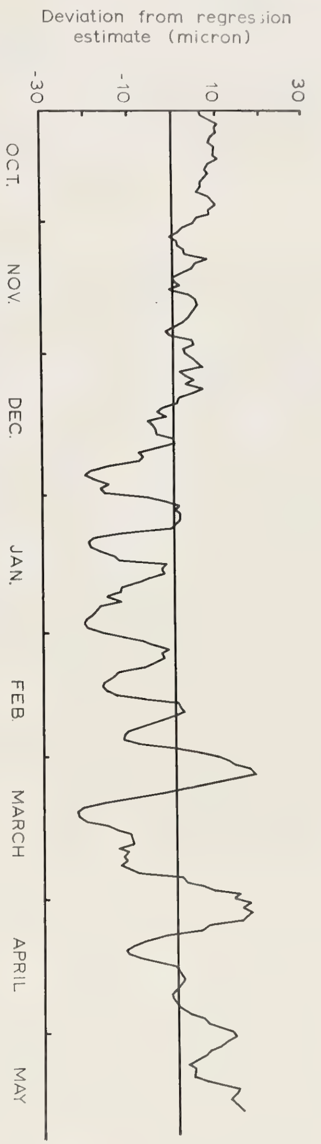

FIG. 2. Deviations from trend curve minus regression estimate, presented as a time series.

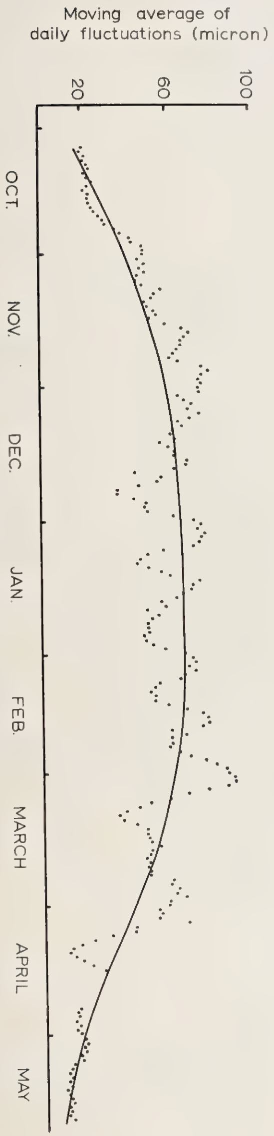

FIG. 1. Moving average of dark fluctuations.

The results are given below:

Lag (days)	serial correlation
1	+ 0,344
2	+ 0,230
3	+ 0,051
4	+ 0,028
5	— 0,102
6	— 0,117
7	— 0,122

The correlation coefficient decreased with increasing interval between the items of the series. The correlation was significantly positive for lags of 1 and 2 days. Hence, a positive deviation from the trend is likely to be followed by a positive deviation during the next 2 days. The algebraic value of the correlation coefficient decreased with increasing lag, but the lowest absolute value was found for a 4-day distance. For a time lag of more than 4 days, the correlation was negative, although non-significant. A level of significance of 0,08 was observed for a lag of 7 days. This indicates that a positive deviation on a given day is likely to be followed by a negative deviation 7 days later. It demonstrates the occurrence of short-term oscillations within the annual cycle. It is also of interest to note that these cyclical variations were most pronounced during the summer months. This must be explained in terms of the more critical water supply during this period. A dry spell during summer will have an immediate and prolonged effect on the internal water balance of the tree and consequently on the magnitude of the diurnal fluctuations. During spring and autumn the soil moisture content is higher, the rate of evapotranspiration lower and the internal water balance more favourable than during summer.

For a study of the influence of external factors, the fluctuations were expressed as a deviation from the trend. This eliminated the necessity to incorporate time as an independent variable. The following variables were introduced into the regression equation:

maximum temperature on the day of measurement (Tmax) average maximum temperature during the preceding 5 days (Tmax(5))

precipitation minus Thornthwaite's evapotranspiration on the day of measurement (P-PET)

precipitation minus evapotranspiration, average value over the last 5 days (P-PET(5)),

all linear interactions between these variables.

The contribution of these variables was tested in a stepwise multiple regression analysis. Tmax, Tmax(5), (P-PET), (P-PET(5)) and the interaction between Tmax(5) and (P-PET(5)) were significantly related with the dependent variable.

The index of multiple determination was 0,545. Unlike earlier studies in *P. radiata*, the results of the regression analysis were not readily interpretable. The regression coefficient for Tmax was positive but those for Tmax(5) and for the interaction between Tmax(5) and (P-PET(5)) were negative. Although there is no doubt about the statistical significance of these variables it is unlikely to reveal a causal relationship. For this reason, some variables were dropped and Tmax and (P-PET) retained in the final equation. The result was as follows:

Diurnal fluctuation (deviation from trend, in micron) =

$$-\ 64{,}4596 + 2{,}6562\ (\mathrm{Tmax}) + 0{,}7649\ (\mathrm{P\text{-}PET}).$$

Temperature is the most influential factor amongst those tested in the regression analysis. With an increase in temperature, the moisture stresses in the tree become greater and the amplitude of the daily cycle increases. The regression coefficient for (P-PET) was positive. This does not necessarily contradict our previous conclusions but is associated with the method of determining the diurnal fluctuation. If during a given day rain occurs after the lowest value of the diameter has been reached, the immediate dehydration and swelling will increase the magnitude of the daily fluctuations measured on the charts. Most frequently the difference between precipitation and water losses will then be positive, partly because the lower temperature on rainy days reduces the rate of evapotranspiration.

For each day during the growing season the difference between the deviation from the trend curve and the regression estimate of this deviation was calculated and presented as a time series (fig. 2).

The average difference must necessarily be equal to zero, because the regression estimates of the deviations were calculated with the method of the least squares. It can be expected that the single values of the time series show randomness, if the regression analyses has been successful to disclose causal relationships. Fig. 2 however indicates that these differences exhibit a time-related trend. During spring, early summer and autumn they tend to be positive and during mid-summer negative. In addition, cyclical variations are retained, indicating that the relationships are more complex and that internal moisture stresses, inducing diurnal fluctuations, cannot be ascribed to environmental influences only.

(2) *Daily growth.*

The period of diameter growth extended from the beginning of October until mid-February and was recorded between 1st October and 19th February. After this date, the trees continued to produce fluctuations but the process of active growth was discontinued. The daily growth was measured as the difference between a chart reading at 8.00 a.m. and 8.00 a.m. on the following day.

Similarly to the analysis of the diurnal fluctuations, 7-day moving averages were calculated and smoothed graphically. The growth record on a given day was expressed as a deviation from this trend curve.

In the regression analysis the daily growth was correlated with:
mean temperature on the day of measurement
mean temperature on the previous day
(P-PET) on the day of measurement and that on the previous day
all linear interactions between these variables.

Tested at the 0,01 level of significance, the analysis of variance was as follows:

Source of variation	degress of freedom	sum of squares	F
X_3	1	19110,58	31,2
X_9	1	11137,00	18,2
X_8	1	4865,12	7,9
residuals	138	84588,69	—

The resulting equation was:

$$Y = - 52{,}889 + 2{,}87718\ X_3 + 0{,}09673\ X_9 - 0{,}07625\ X_8$$

where: X_3 = mean temperature (°C) on the previous day
X_9 = (mean temperature on the previous day) × (P-PET on the day of measurement)

X_8 = (mean temperature on day of measurement) × (P-PET on previous day)

Y = growth in micron (deviation from trend).

The index of multiple determination was 0,293. The regression coefficients for X_3 and X_9 were positive. In the regression analysis, X_3, the mean temperature on the preceding day appeared to be the most influential environmental factor. In addition a combination of a high temperature on the previous day and a moisture surplus on the current day was positively related to growth. The variable X_8, which expresses the influence of the interaction between mean temperature on the day of measurement and (P-PET) on the previous day and evaluates the relationship independently of those existing between Y and X_3, and X_9 respectively, was negatively related to growth. It is difficult to interpret this negative regression. Possibly, the difference between precipitation and water losses by vaporization, calculated with Thornthwaite's method does not satisfactorily express the water balance of the tree. A combination of a high temperature on the day of measurement and a moisture surplus on the previous day might eventually be inhibiting for growth, because of soil moisture depletion, associated with periods of high temperature.

The approach in the present study has certain short-comings. Instead of calculating the difference between precipitation and atmospheric water losses, it might be more useful to obtain a continuous record of the fluctuations of the soil moisture content. In addition, it has been found that the multiple regression analysis may give results, which are difficult to interpret. Growth is a highly complex phenomenon, which is causally influenced by the physical environment of the tree, but also by other, internal factors, which in turn may be related to environmental factors, ignored in the growth study.

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A NEW SPECIES OF *GLADIOLUS* AND SOME NOMENCLATURAL CHANGES IN THE IRIDACEAE

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Abstract

A new species *Gladiolus lapeirousioides* is described. This is followed by a short discussion of the rules of nomenclature dealing with superfluous names. Five species of Cape Iridaceae are dealt with in this connection. The names of *Ixia crispa*, *Hexaglottis flexuosa* and *Aristea caerulea* (*coerulea*) are illegitimate and the new names *Ixia erubescens*, *Hexaglottis lewisiae* and *Aristea monticola* are proposed.

Uittreksel

'N NUWE SOORT *GLADIOLUS* EN 'N PAAR NAAMVERANDERINGS IN DIE IRIDACEAE.
'n Nuwe soort *Gladiolus* word beskryf. Dit word gevolg deur 'n kort bespreking oor die nomenklatuur reëls wat met oorbodige name handel. Vyf soorte Kaapse Iridaceae word in hierdie verband behandel.

1. A New Species Of Gladiolus

Gladiolus lapeirousioides Goldbl. sp. nov. Holotype: *Goldblatt* 540 (BOL); isotypes NBG, PRE.

Species proprie, foliis falcatis tribus, inflorescentia inflexa et perianthii tubo gracile longo distinguitur.

Planta parva, ad 15 cm alta. Caudex cormus conicus, ad 2 cm longus, bulbiliferus, tunicis exterioris longitudinaliter fissuris. Folium vaginans unum, membranaceum. Folia basalia 3—4, falcata, ad 15 cm longa et 0,4 cm lata. Scapus simplex vel pauciramosus, ad basem inflorescentiae inflexus. Inflorescentia spica secunda, ad 8—10 flores composita. Bracteae duae, herbaceae, 1—15 cm longae, exterior longior interior inclusa. Flores zygomorphes, cremei ad subrosei et rubri punctati; perianthii tubus 3—4 cm longus, gracilis; perianthii segmenta ovata ad lanceolata, inaequalia, superior magnum lateralia reflexa, inferiora tria minora, et quoque rubro notata propre basem. Stamina erecta, antherae unilaterales contiguae. Stylus filiformis, ramosus ad apicem antherarum, rami ad apices expansi et bilobi. Capsula ovoidea, 1 cm longa, pauca semina alata continens.

Plants fairly small, reaching to 15 cm above the ground. Corm conical, up to 2 cm long, tapering at the apex, base rounded, inner tunics entire and light yellow, outer tunics light brown, and split from the base into a number of strips,

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bearing cormlets round the base and on the ends of short runners. Sheathing leaf only one, membranous, reaching to ground level. Basal leaves three, distichously arranged, equitant, 2,5—4 mm wide, up to 15 cm long, falcate, midrib prominent. Scape simple or bearing one or two branches; terete, inflexed below the inflorescence. Cauline leaves subtending each branch, or if scape simple, then inserted shortly above the ground. Inflorescence a secund spike, held more or less parallel to the ground, bearing up to 10 flowers. Bracts two, inner slightly shorter and enclosed in the outer, herbaceous, 1—1,5 cm long, acute. Flower zygomorphic, cream coloured; perianth tube 3—4 cm long, slender, but widening very gradually towards the apex; perianth segments unequal, narrowly ovate to lanceolate, upper segment largest, erect, upper lateral segments reflexed, lower three segments smallest, forming a lip, each marked near the base with a red spot. Stamens erect, inserted at the apex of the perianth tube, cream coloured, anthers unilateral and contiguous. Ovary ovoid, about 0·3 cm long, style filiform, three-branched, branching at the level of the anthers, stigma at the end of each branch, expanded and bilobed. Capsule ovoid, about 1 cm long, each loculus containing only a few seeds; seeds light brown, winged.

FIG. 1.
Gladiolus lapeirousioides in flower at the type locality, south-east of Loeriesfontein, Cape Province.

Flowering time: September.

Habitat: In decomposed shale at the base of hills in the area south of Loeriesfontein.

Material examined:

CAPE—30 19 (Loeriesfontein): south of Loeriesfontein, about 1 mile along turnoff to Kliprand from the Loeriesfontein-Nieuwoudtville road (-CD), *Goldblatt* 540 (BOL, NBG, PRE).

The inflexed inflorescence and the flower with its long narrow perianth tube and extended segments distinguish this species from all other representatives of the genus. The small capsule containing comparatively few winged seeds is also very characteristic.

This very unusual and very distinct species was discovered in full bloom in the spring of 1970 in the dry, arid area south of Loeriesfontein. Superficially it is very similar to *Lapeirousia fabricii*, a plant that the author was actually searching for when this *Gladiolus* was discovered. From a distance the two look very similar, having flowers of the same colour and structure. Closer examination revealed that it was actually a *Gladiolus* as it has a round based corm covered by rather papery tunics and, of course, lacks the divided style branches typical of *Lapeirousia*. There was initially some difficulty over deciding the correct genus to which the plant should be assigned. A later visit to the area yielded fruiting material. Although the capsules are rather small and contain rather few seeds for *Gladiolus*, the characteristically winged seeds left no doubt about the correct genus.

When examined in detail, *G. lapeirousioides* proved to be unlike any known species of *Gladiolus* and as far as could be discovered had not previously been collected. This appears to be rather surprising as the locality, between Loeriesfontein and Nieuwoudtville, is close to a well used road. The explanation may lie in the fact that this arid area receives very infrequent rains and the plant may flower very irregularly, in seasons when the rainfall has been sufficient.

2. Notes on Nomenclature

Superfluous Names.

Article 63 of the International Code of Botanical Nomenclature (1966) deals with the problem of superfluous names. This has given, and will continue to give South African botanists a great deal of trouble for a considerable time to come. Many of our well-known plants have names that can or must be considered superfluous. The rule states that a name is illegitimate and must be rejected if it was nomenclaturally superfluous when published. According

to the article this means that if the supposed new taxon *as circumscribed by the author*,* included the type of a name or epithet which ought to have been adopted, the new taxon must be rejected.

The inclusion of a type is understood to mean the citation of a type specimen or its illustration, or the citation of the type of a name or the name itself unless the type is at the same time excluded . . . *either explicitly or by implication*.* This last phrase was added to the article at the 1969 Seattle International Botanical Congress and published in *Taxon* (Stafleu 1970). The intention was to make it clear that automatism in rejection of names was not necessary. Indeed, according to Stafleu a name is not automatically superfluous if the type of the cited name could not within reason have been included by the author within the circumscription of his new taxon. Thus, automatic mistypification (article 7 note 4) is avoided and in some cases the so-called superfluous name is acceptable.

Although it is now clear that rigid application of the rule is unnecessary, it does not allow much flexibility when dealing with early authors such as Thunberg or the younger Linnaeus who, on occasion, cited earlier synonyms for their new taxa. While these are obviously cases of misidentification, it is quite clear that with their incomplete knowledge of the flora and their frequent ignorance of the actual type specimen, they were acting in good faith and believed the two to be identical. Descriptions were at that time frequently inadequate and often it is quite impossible to find any inconsistency in the circumscription of either species which would reveal that two instead of one taxon was involved. Thus, it can seldom be argued that the earlier synonym did not fit the circumscription of the new taxon or that the type specimen was excluded even by implication. If such inconsistencies could be found then it would become possible to argue the legitimacy of an otherwise superfluous epithet.

In the present paper five species of Iridaceae are dealt with. In three cases the present author has found it necessary to reject well-known names for quite common Cape plants. The species concerned are *Ixia crispa* L.f., *Aristea caerulea* (Thunb.) Vahl (also spelled coerulea) and *Hexaglottis flexuosa* (L.f.) Sweet. *Anapalina caffra* (Ker ex Bak.) Lewis and *Babiana disticha* Ker (= *plicata*) are also dealt with in this connection.

1. *Ixia crispa* L.f.

The plant known as *Ixia crispa* L.f. requires renaming as the younger Linnaeus (1781) cited as a synonym *Ixia undulata* Burm. f. (1766) when he first described the plant. For a long time these two species were believed to be

*Author's italics.

identical, but N. E. Brown (1929) in his study of Burman's herbarium saw that *Ixia undulata* was quite distinct. At that time the two names were regarded as synonyms of *Tritonia undulata* (Burm. f.) Bak. Brown decided that the plant typified by the younger Linnaeus' *I. crispa* should be transferred to *Tritonia*. As it would have been a homonym of *T. crispa* (L.f.) Ker, he named it *Tritonia thunbergii*.

When Dr. G. J. Lewis revised the genus *Ixia* in 1962 she transferred several species of *Tritonia*, belonging to the subgenus *Dichone* to *Ixia*, among them, *T. thunbergii*, which automatically became *Ixia crispa* once more. As the epithet is superfluous and the only available synonym, *T. thunbergii* is occupied in *Ixia*, a new name, *Ixia erubescens* is proposed.

Strictly speaking, *Ixia crispa* L.f. is a nomenclatural synonym of *Ixia undulata* Burm. f., but it is included in the synonymy of *Ixia erubescens* as the description and specimen cited apply to the latter and not to Burman's plant. The type specimen and description of *Ixia erubescens* remain those of the younger Linnaeus, as there is no intention to alter the species as he described it, except to exclude the cited synonym *Ixia undulata*. Other synonyms bearing the specific epithet *crispa* are also included as these were intended to apply to the younger Linnaeus' plant.

Ixia erubescens Goldbl. nom. nov.

Ixia crispa sensu L.f., Suppl.: 91 (1781), as to description and specimen cited but not to synonym; nom. illeg. (nom. superfl.); sensu Lewis in Jl S. Afr. Bot. 28: 166 (1962).
Type: *Thunberg* 313 (LINN, holo).
Agretta crispa (L.f.) Eckl., Top. Verz.: 24 (1827).
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Tritonia thunbergii N.E.Br. in Kew Bull. 1929: 137 (1929).

2. *Hexaglottis flexuosa* (L.f.) Sweet.

This plant was first described as *Moraea flexuosa* by the younger Linnaeus who cited as a synonym the earlier name *Ixia longifolia* Jacq. The latter plant is very similar to *Moraea flexuosa* and they were often regarded as identical. Two species are, however, involved. When Sweet transferred *M. flexuosa* to *Hexaglottis*, he cited and continued to regard *Hexaglottis longifolia* (based on *Ixia longifolia*) as a synonym. The epithet is thus superfluous in both genera and must be rejected. As there are no legitimate synonyms available, a new

name is proposed. The name *H. lewisiae* was chosen in honour of Dr. G. J. Lewis for her excellent work on the South African Iridaceae.

Moraea flexuosa L.f. is a nomenclatural synonym of *Ixia longifolia* Jacq. (and of *Hexaglottis longifolia* (Jacq.) Vent.), but is included here in the synonymy of *Hexaglottis lewisiae* as the specimen cited by the younger Linnaeus is the latter species and the description applies equally well to this as to *Hexaglottis longifolia*. The type of *H. lewisiae* remains the lectotype chosen by Lewis (1959) for *H. flexuosa*.

Hexaglottis lewisiae Goldbl. nom. nov.

Moraea flexuosa sensu L.f. Suppl.: 100 (1781) as to specimen cited but not to synonym; nom. illeg. (nom. superfl.).

Hexaglottis flexuosa (L.f.) Sweet, Hort. Brit. ed. 2: 498 (1830), excluding synonym *Hexaglottis longifolia* (Jacq.) Vent.; nom. illeg. (nom. superfl.); sensu Lewis in Jl S. Afr. Bot. 25: 233 (1959).

Type: *Thunb.* in Herb. Thunb. 1217 (UPS, lecto).

3. *Aristea caerulea* (Thunb.) Vahl.

Both Thunberg, who first described *Moraea caerulea* and Vahl who transferred it to *Aristea*, cited *Gladiolus capitatus* L. as a synonym. There is little doubt that *Gladiolus capitatus* was an *Aristea* but its exact identity is not known due to the absence of a type specimen and the inadequate description. Thus it is not known whether Thunberg was correct in regarding *Moraea caerulea* and *Gladiolus capitatus* as conspecific or not. In either event, *Moraea caerulea* must be rejected. The specific epithet is often spelled "coerulea", which is probably an orthographic variant of Thunberg's spelling, though the reason for this is not known to the present author. In the absence of any known legitimate synonyms (Weimarck 1940), a new name *Aristea monticola* is proposed. The type for this species remains the Thunberg specimen of *Moraea caerulea* as chosen by Weimarck.

Aristea monticola Goldbl. nom. nov.

Moraea caerulea sensu Thunb., Diss. Moraea: 12 (1787) as to description and specimen but not to synonym; nom. illeg. (nom. superfl.).

Aristea caerulea (Thunb.) Vahl, Enum. 2: 124 (1805), excluding synonym *Gladiolus capitatus*; nom. illeg. (nom. superfll.); sensu Weimarck in Lunds Univ. Arssk. N. F. Avd. 2, 36: 1 (1940).

Type: *Thunb.* in Herb. Thunb. "*Moraea flexuosa* a" (cf. Wiemarck 1940) (UPS, lecto).

4. *Anapalina caffra.*

This species, long included in other species of the same genus, was first described by Baker in 1892 as *Antholyza caffra.* Baker cited Ker as the author, although Ker published the name without description and the identity of Ker's plant is not certain. Baker also cited *Anisanthus splendens* Sweet (1831) as a synonym, though this was a misidentification. Although similar, this plant actually belongs to a quite different genus. *Antholyza caffra* must be regarded as having been published in 1892, long after *Anisanthus splendens* and thus appears to be superfluous. It is, however, quite clear from Baker's description that *Anisanthus splendens* as figured and described by Sweet does not fall within the circumscription of *Antholyza caffra.* As Baker probably named his plant *A. caffra,* thinking Ker's name had priority over *Anisanthus splendens* and because the latter cannot be included in Baker's circumscription of the species the question of superfluity cannot really be raised, particularly if Stafleu's interpretation of the modification of article 63 is followed. The citation of the species should, however, read *Antholyza caffra* Ker ex Baker and *Anapalina caffra* (Ker ex Baker) Lewis.

5. A note on *Babiana plicata,* correctly *B. disticha.*

Babiana plicata Ker, the type species of the genus *Babiana,* was shown by Bullock (1961), in his review of Lewis' monograph of *Babiana,* to be illegitimate because *Gladiolus fragrans* an available synonym, was cited by Ker and is in fact the same species. As Bullock pointed out, the epithet *fragrans* is preoccupied in *Babiana* so that *G. fragrans* cannot be transferred to this genus and the taxonomically correct name for the taxon is *Babiana disticha* Ker in Bot. Mag.: t. 606 (1803).

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A NOTE ON THE DIATOM *THALASSIOTHRIX VANHOEFFENI* HEIDEN & KOLBE, WITH REFERENCE TO SPECIMENS FOUND IN THE AGULHAS CURRENT

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ABSTRACT

An account is given of variations in the morphology of specimens of the diatom *Thalassiothrix vanhoeffeni* Heiden & Kolbe found in the Agulhas current, together with electron micrographs of part of the valve of a specimen.

UITTREKSEL

AANTEKENINGE OOR DIE DIATOOM *THALASSIOTHRIX VANHOEFFENI* HEIDEN & KOLBE, MET VERWYSING NA MONSTERS WAT IN DIE AGULHAS SEESTROOM GEVIND IS. Die verslag handel oor verskille in die morfologie van sekere monsters van die diatoom *Thalassiothrix vanhoeffeni* Heiden & Kolbe, wat in die Agulhas seestroom gevind word, tesame met elektron mikrograwe van 'n gedeelte van die monster se klep.

INTRODUCTION

Thalassiothrix vanhoeffeni was first described by Heiden and Kolbe (1928) from Atlantic samples from latitudes 8° 5′ S. to 30° 49′ S. The type description is given below:

"Valves linear, at one end bluntly rounded, with a bordered pore and stigma, at the other end tapering, wedge-shaped, rounded with a stigma; length 990–2040μ, valve width 3μ. Valve with short marginal grooves on both sides, 85–100 in 100μ, each with a granule. The pseudoraphe is linear, $\frac{1}{3}$ of the valve width, abruptly narrowed at the wedge-shaped end. At the blunt end of the valve, there are short marginal striae instead of marginal grooves, at the other end, fine puncta over the whole surface of the valve. Girdle width 4–6,6μ, with one end wedge-shaped and pointed, the other truncated, slightly constricted. The marginal grooves on the valve extend onto the girdle side. The cells are rectangular in transverse section and sometimes twisted up to 90° about the longitudinal axis."

The only other illustration of *T. vanhoeffeni* appears to be that of Hasle (1960) and the only other records of the species are in checklists of Taylor (1967) and Thorrington-Smith (1969).

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Taylor (1964 Ph.D. Thesis) recorded the species in samples from only two stations in the S.W. Indian Ocean, but suggested that *T. vanhoeffeni* could be confused with *T. acuta* Karsten. Karsten (1905) described *T. acuta* as follows: "4–5: 1600μ. Cell twisted so that one end shows the valve side, the other the girdle side; thus this belongs to the genus *Thalassiothrix*. Both valve ends pointed. Valves with pseudoraphe and 11–12 transverse striae in 10μ." The figure shows the pointed or foot end in valve view, with transverse striae extending right to the apex and the pseudoraphe a thin line. Hendy (1937) described *T. acuta* as having a "narrow and indistinct pseudoraphe". Thus only in the number of transverse striae in 10μ is there any similarity between the two species. *T. acuta* was not found in samples from Agulhas current NGY stations, but it has been recorded in checklists for the W. and S.W. Indian by Taylor (1967), Nel (1968) and Thorrington-Smith (1969 and 1970).

There are some features of similarity between *T. vanhoeffeni* and *T. elongata* Grunow ex Allen & Cupp. *T. elongata* appears to have been illustrated only twice and both figures are unfortunately poor. The description of Allen and Cupp (1935) is given: "Cells single threadlike. Valves very long, slightly curved; one end slightly pointed, the other rounded. Marginal striae 9–14 in 10μ . . . Length 1054–1260μ; width 3–4μ." Allen and Cupp considered *T. elongata* "closely related to or possibly a synonym of the usually more northerly *T. longissima* Cl. & Grun." The only other records of *T. elongata* appear to be in checklists of Wood (1962) and Nel (1968).

T. vanhoeffeni in NGY samples from the Agulhas current

Cells agreeing with Heiden and Kolbe's description of *T. vanhoeffeni* were found at 61 out of 76 samples from NGY stations in the Agulhas current collected during International Geophysical Year 1958. (For the hydrographic data of the NGY stations see Zoutendyk 1960.)

Calculating frequency as a percentage for each sample, the maximum percentage frequency for *T. vanhoeffeni* was 2%; in half of the samples in which it was recorded, it was 0,33% or less.

The specimens attributed to *T. vanhoeffeni* differ from Heiden and Kolbe's

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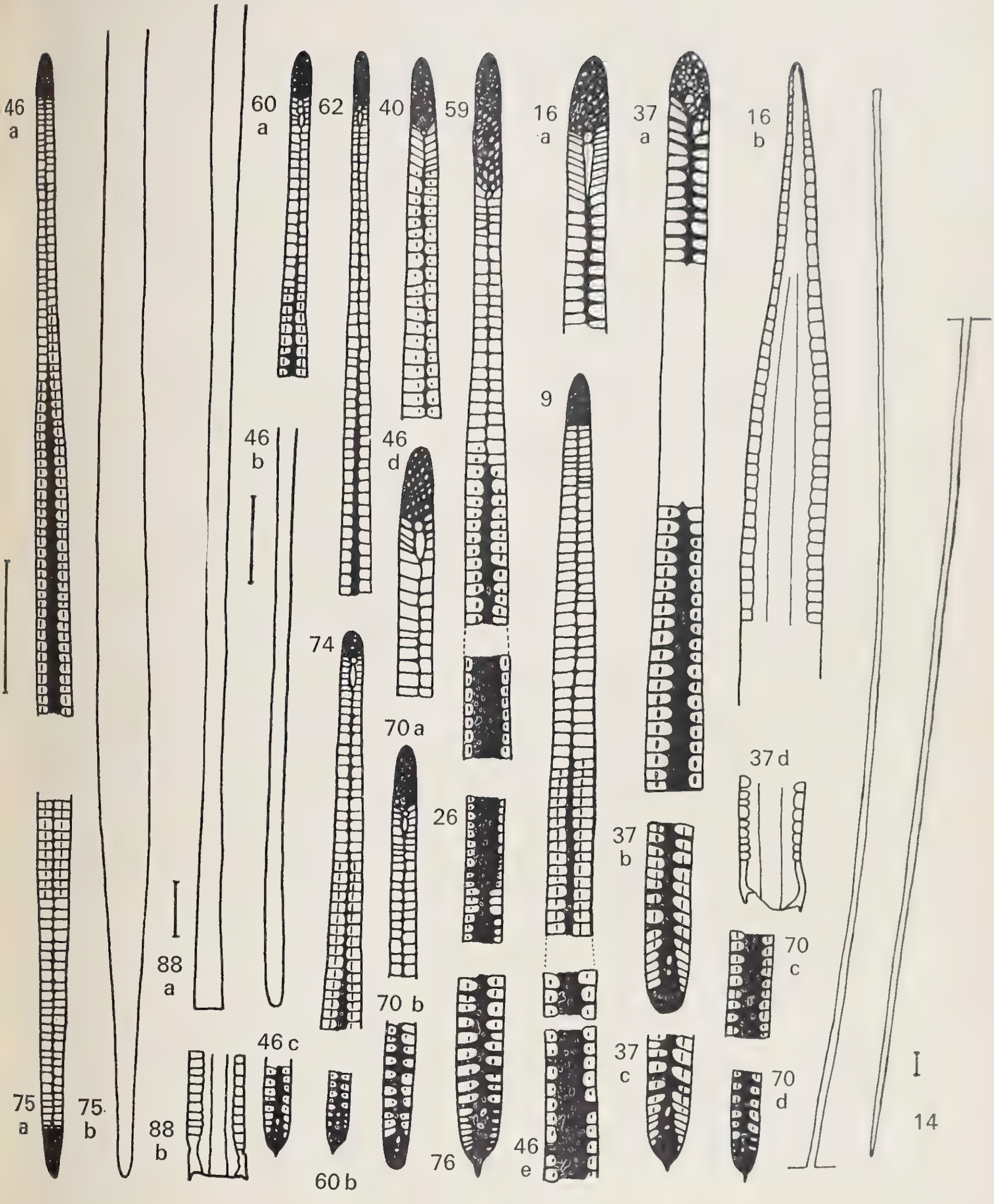
Fig. 1.

Thalassiothrix vanhoeffeni. (Specimens numbered according to NGY stations at which they were found.) *14*, entire cell in girdle view; *9*, *40*, *59*, *62* and *74*, valve views of foot or basal end showing variation in patterning of apical part of valve; *26*, valve view of mid valve showing unusual long marginal grooves; *76* valve view of head end; *16 a* and *b*, valve and girdle view of foot; *37 a*, foot, *b* and *c*, head ends of valves, of same cell; *d* head end in girdle view; *46 a*, foot end; *b* and *c*, head end of second cell; *d* and *e*, foot and mid cell in valve view of third specimen; *60 a* and *b*, foot and valve of same cell; *70 a*, *b* and *c*, foot, head and mid body of same cell; *d*, foot of second cell; *75 a* and *b*, foot in valve and outline girdle view; *88 a* and *b*, head in girdle view. The scale line indicates 10μ. Camera lucida drawings, all to same scale except *14*, *46 b* and *88 a*.


46 a
60 a
62
40
59
16 a
37 a
16 b
46 b
46 d
9
74
70 a
37 d
26
37 b
88 a
70 c
70 b
46 c
37 c
70 d
14
75 a
75 b
88 b
60 b
76
46 e

original description in showing a greater range in the number of marginal markings in 10μ, and variability in the valve markings in the region of the foot.

EXPANDED DESCRIPTION OF *T. vanhoeffeni* HEIDEN & KOLBE (See Fig. 1)

T. vanhoeffeni differs from other species of *Thalassiothrix* in the slighter torsion and curvature of the cell, in the number of marginal markings or grooves per 10μ, in the presence of an elongated bar in each groove, in the absence of marginal spines, in the broad central area and in the valve structure in the region of the foot.

Torsion of cell: the cell may be curved in a slight arc and slightly twisted about the longitudinal axis, but only in one instance was this torsion as much as 90°, so that one end of the cell was seen in girdle view, the other in valve view.

Length of cell: 621–2070μ.

Dimensions and shape in girdle view: the head of the cell is truncate, 3,2–6,0μ wide at the end, tapering over 50–70μ to a width of 2,4–3,6μ; the cell then enlarges gradually to a maximum girdle width of 3,2–8,0μ and tapers gradually to a width of 2,8–5,6μ at a distance of 130–300μ from the posterior or basal end, also referred to as the foot, enlarging again to a width of 3,6–6,4μ and then tapering over a distance of 25–35μ to a somewhat drawn-out point.

Dimensions and shape in valve view: the head is rounded, 2,5–4,0μ wide, narrowing at about 50–70μ behind the tip to a width of 1,5–3,0μ, then enlarging gradually to a width of 3,0–4,5μ and tapering again towards the basal foot with the valve width of the attenuated end 1,5–4,0μ; the end of the foot is rounded.

Markings of valve: the valve is ornamented by what Heiden and Kolbe termed "marginal grooves", and in descriptions of other species of *Thalassiothrix* are referred to as transverse or marginal striae, which extend onto the mantle; each groove has an elongated bar, referred to by Heiden and Kolbe as a "granule". The marginal grooves border a central unmarked area, referred to as the pseudoraphe by earlier authors, but better termed the central area, occupying two thirds of the valve width for most of the valve length, but narrowing abruptly in the region of the foot, in the attenuated part of which it becomes a thin line bordered by marginal grooves in which the "granule" is indiscernible. The valve markings of the apical part of the foot vary: the central area may be terminated by an elongated "patch", the "stigma" of Heiden and Kolbe, with a rounded "patch" lying immediately in front of it; sometimes only one of the patches terminating the central area is present, sometimes neither is discernible under the light microscope; beyond this, the rest of the valve is marked all over with small puncta, whose size, arrangement and number are generally not easily seen. In the region of the head, the central area does not narrow much, and it is terminated by a round "patch", the "pore" of Heiden

and Kolbe, generally immediately anterior to an elongated or rounded "stigma"; the former is always present, but the position and presence of the latter varies; the patterning of the valve beyond this is not easily seen: it appears to consist of smaller, less regularly arranged marginal puncta. The apex of the head may bear a single small spine. The number of marginal grooves in 10μ varies from 8–9 in a specimen to 13–14 in a specimen, mostly 11, with the marginal grooves in 10μ more numerous in the region of the foot. Gaps in the marginal grooves may occur, and rarely, a few grooves are found, projecting into the central area.

ELECTRON MICROSCOPE OBSERVATIONS OF *T. vanhoeffeni*. (See Fig. 2.)

Hasle (1967) has shown that in *T. longissima* and *T. antarctica* Schimper, the transverse striae correspond to a series of marginal depressions, with less heavily silicified walls, seen in *T. longissima* to be thickened with a reticulate pattern, with an internal opening in each depression and with the concavity of the depression orientated towards the inside of the valve. The depressions alternate with narrow low marginal ribs.

Examination under the electron microscope of species never present in large numbers is difficult, and it was fortuitous that a portion of the foot end of a valve was included in an E.M. preparation.

In this specimen, in the region of the attenuated point, the marginal depressions did not appear to extend onto the mantle. Both the elongated "stigma" and round "patch" terminating the central area were present, but the tip of the valve posterior to this was broken. Where the central area began to widen, the marginal depressions extended onto the mantle and were traversed by bars of wall material of the same density as the central area and parallel to it. These bars were incomplete in the first few depressions, but anteriorly they divided each depression into three compartments, two of which would be visible in valve view under the light microscope, the dividing bar forming the "granule" of Heiden and Kolbe. The wall between the marginal depressions appeared to be slightly denser than the central area, but not raised in transverse ribs as in *T. antarctica* (Hasle l.c. fig. 45). The much thinner wall of the marginal depressions had disintegrated in most depressions and it was not possible to see the exact nature of the thickening, or the internal openings.

A second fragment was found, which could be a portion of the head end of a valve of *T. vanhoeffeni*, but this is by no means certain, as the central area was narrower than generally observed in specimens under the light microscope. The marginal depressions around the end of the central area were irregularly divided into a number of compartments by bars of wall material, less dense and at a slightly different level to the central area and the parts of the valve between

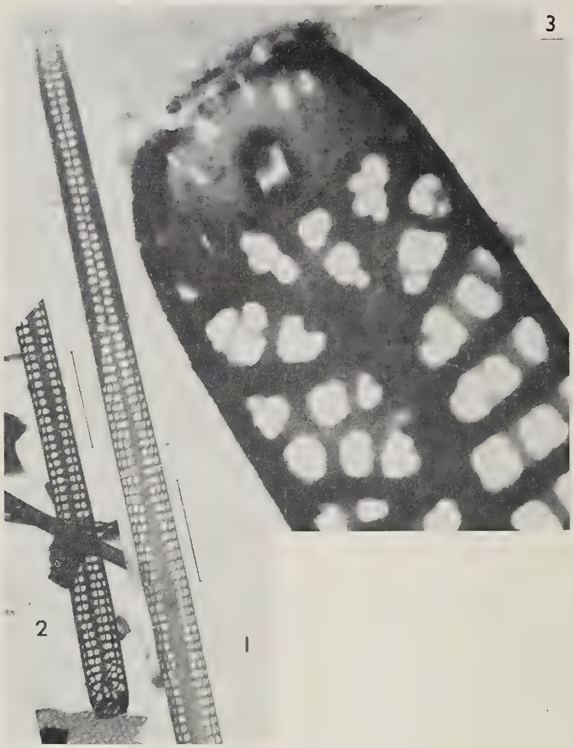


Fig. 2.

1. Electronmicrograph of foot or base end of valve of *T. vanhoeffeni*, apex of valve missing; 2, electronmicrograph of putative head end of valve of *T. vanhoeffeni;* 3, the same greatly enlarged. The scale line indicates 10μ.

the compartments. Each compartment was traversed by a ramification of even less dense wall material at yet a third level. A definite pore with a thickened rim was evident, posterior to which was a depression divided into two compartments, which under the light microscope might appear as the "stigma" of Heiden and Kolbe. The end of the valve was perforated by smaller pores, which in valve view under the light microscope would appear marginal. Further back, the depressions were divided into three compartments by bars parallel to the central area, and at about 18µ from the apex, into two compartments.

ACKNOWLEDGMENTS

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The Biology of Parasitic Flowering Plants by Job Kuijt, with pp. 246, figs. 187. University of California Press, 1969. £7.3 (U.K.).

Aside from Christmann's excellent little book, "Le parasitisme chez les plantes", there is no recent survey of angiospermous parasites. The present work is claimed to be a synthesis of virtually everything of significance that is known about this fascinating group of organisms. It does indeed provide a comprehensive and well documented account, encompassing such varied aspects as taxonomy, morphology, development, biology, physiology and even, in a most entertaining way, mythology.

Although the arrangement of this book is broadly systematic, there are separate chapters dealing with the haustorium, the physiology of parasitism and with possible lines of evolution of angiospermous parasites. An encyclopaedic work of this nature is always valuable in that it draws attention to what remains to be done. The reader will be impressed by what has been accomplished during the last fifteen years but will also be brought to realise how much more there remains to be discovered about the more interesting parasites of Southern Africa.

This book is written in a lively and provocative style and the author's extensive contributions and dynamic personality are much in evidence. There is a profusion of clear and beautifully executed illustrations and the general standard of production is of a very high order.

A. R. A. Noel

Cell Division and Heredity by Roger Kemp, with pp. 47, figures 27, 4 plates and 15s. boards. The Institute of Biology's Studies in Biology No. 21. London: Edward Arnold, 1970. 9s. paperback.

It is to a large extent true that an understanding of the principles of Mendelism and of the mechanism of meiotic division enables one to pursue the study of genetics to quite an advanced level. Descriptions and analyses of Mendels' experiments are now widely available but discussions of the full significance of meiosis, apart from purely cytological features, are often rather summarily treated in elementary texts. This present work is therefore to be welcomed in that it establishes, in a simple and direct fashion, the central position of meiosis in the general scheme of genetic transmission. A further desirable innovation is that this relationship is based, wherever possible, on tetrad analysis in the fungi, a much more logical and easily demonstrated approach than is possible with the classical pea experiments. This book also includes sections on chromosomal mutations and breeding systems, the latter introducing the concept of population genetics and the mechanism of selection.

This book will be useful in the higher grades at school and in first year university courses.

A. R. A. Noel

The Cuticles of Plants by J. T. Martin and B. E. Juniper, with pp. xx + 347, with 78 line and half tone illustrations. London: Edward Arnold, 1970. £7.5.0.

The Authors and publishers are to be congratulated for having most successfully filled an outstanding gap in botanical literature. It would be difficult to find elsewhere such a comprehensive treatment of the cuticle and Martin and Juniper's book will certainly become the standard reference work on this much neglected feature of plants.

The reason for this neglect has undoubtedly been the supposed simplicity of structure and functions of the cuticle. The present work dispels this misconception and, written in a concise and highly readable style, the description of the all-important boundary between the plant and the external environment fills a fair-sized book.

There are four main approaches. viz: methods of study, with special reference to electron microscopy; structure and development; chemistry, biosynthesis and decay; functions. So many aspects are covered that only a few can be specifically mentioned. The section on chemistry is well done and discloses the great variety of composition of the cuticle, cutinised and corky walls, including some mention of taxonomic significance. There

is an important discussion of the basis of wetting and penetration by sprays, as well as an account of the interaction between micro-organisms and the cuticle. There is a good summary of recent ideas on the cuticular control of water loss, and of its significance in the environment. The bibliography is extensive and the book is well indexed. The general standard of production is high and the numerous excellent electron-micrography are very well printed.

A. R. A. Noel

Turfgrass Science ed. by A. A. Hanson and F. V. Juska, with pp. 715, 160 figures, 73 tables. Madison: American Society of Agronomy, 1969. $12.50.

This work is what the title suggests—a scientific treatise on turfgrass written by thirty-eight different authors and edited by two leading scientists from the famous American research station at Beltsville.

The introductory chapters on the history of turf usage and the turfgrass industry make one realise what a big business turf production has become in the United States.

There are most important and interesting discussions on climate and soils and the adaptation of different species and ecotypes of grasses to these in different parts of the country. Detailed discussions on the nutrition of turfgrasses and their fertiliser requirements are given together with the effects of mineral deficiencies and toxicity.

Soil water and its effect on turf are discussed and the irrigation management of turf, particularly the determination of the frequency and amount of irrigation—something of extreme importance in the management of golf and bowling greens—is dealt with.

The subjects of physiology of growth and ecology lead up to a very good discussion on management. Very useful sections follow on turf weeds, turfgrass diseases, many of which occur in South Africa, harmful insects and other pests and their control.

Species and strains of turfgrasses and their suitability in different parts of the United States are dealt with but little of this is applicable in South Africa. The same remarks apply to the chapters on turfgrass improvement and production of seed.

Seedbed preparation and planting, as described, is of much importance but, again, the conditions of climate under which they are carried out, do not necessarily apply to our South African conditions.

The management of putting greens, golf fairways and roughs, and highway roadsides is of fairly general application while the chapter on equipment for turf is most useful.

This book is a "MUST" for all students of turf and turf management. It is a first class textbook written in scientific and readable language. It is not just a handbook on "do's and don'ts" in management but it gives the whole scientific background for all practices in turf management. Committees of management for golf and bowls clubs would do well to acquire and study the book.

J. D. Scott

INSTRUCTIONS TO CONTRIBUTORS TO THE JOURNAL OF SOUTH AFRICAN BOTANY

This Journal provides a medium for the publication of the results of botanical research primarily on the flora of Southern Africa, whether systematic, morphological, ecological or otherwise and whether carried out in South Africa or elsewhere. Papers on botanical subjects of special interest and application in South Africa may be included.

Contributions must be original and should not be translations of previously published papers.

Papers must be submitted in final, corrected form. They are accepted for publication on the recommendation of the Editorial Committee.

Authors may be charged expenses for corrections if alterations are excessive.

COPY

Papers should be type-written, double spaced throughout on one side of the paper and with margins of at least 3 cm (1 inch). Footnotes and elaborate tables should be avoided. Latin binomials should be underlined once to indicate italics. All other marking of copy should be left to the Editor. The original, plus at least one carbon copy, must be submitted.

GENERAL LAY-OUT

Each paper should be headed with a concise informative **title** in capitals with the author's name below. This should be followed by the name of the institution, where the work was carried out, underlined and placed within brackets.

A concisely written **abstract** in English and Afrikaans, of not more than 200 words, should precede the text.

The subject matter should be divided into sections under short appropriate **headings** such as: INTRODUCTION, MATERIAL AND METHODS, RESULTS, DISCUSSION CONCLUSION, ACKNOWLEDGMENTS, etc.

Tables and **illustrations** should be on separate sheets. **Figures** and **graphs** should be in Indian ink on white card or Bristol board. Lettering for figures can be inserted by the printers in which case authors should indicate the desired lettering on the original figure lightly in pencil. The maximum dimensions available for figures are 18 cm $\times$ 12 cm (7″ $\times$ 4½″). Line drawings for blocks should be at least twice the size they will be when reduced for publication. All figures should be supplied with a scale. The most suitable method of indicating magnification is a scale line (in metric units) incorporated in the figure. Photographs for half-tone reproductions should be on glossy paper, clearly marked on the reverse side (in pencil) to indicate the top. Line drawings and half-tone illustrations are termed figures and should be numbered consecutively. Captions for figures should be typed on a separate sheet of paper.

TAXONOMIC PAPERS

Authors must adhere to the International Rules of Botanical Nomenclature. **Abbreviations of herbaria** must be cited in accordance with the most recent edition of Index Herbariorum, Pt 1 (The Herbaria of the World, 5th ed., 1964). When **new species** are described, the exact location of type material must be indicated. When proposing **new combinations** the full citation of the basionym is required. **Indented keys** with numbered couplets are preferred when dealing with a small number of taxa. **Bracket keys** should be used when dealing with a large number of taxa. When citing **synonyms** they should be arranged chronologically into groups of nomenclatural synonyms and these should be

arranged chronologically by basionyms. Whenever possible, the types of the basionyms should be cited, e.g.:

Bequaertiodendron magalismontanum (Sond.) Heine & J. H. Hemsley in Kew Bull. **1960**: 307 (1960).
Chrysophyllum magalismontanum Sond. in Linnaea **23**: 72 (1850). Type: Magaliesberg, *Zeyher*, 1849 (S, holo; BOL!, SAM!).
Zeyherella magalismontana (Sond.) Aubrév. & Pellegr. in Bull. Soc. bot. Fr. **105**: 37 (1958).
Pouteria magalismontana (Sond.) A. Meeuse in Bothalia **7**: 335 (1960).
Chrysophyllum argyrophyllum Hiern, Cat. Afr. Pl. Welw. **3**: 641 (1898). Syntypes: Angola, *Welwitsch* 4827, 4828, 4829 (BM!).
Boivinella argyrophylla (Hiern) Aubrév. & Pellegr. in Bull. Soc. bot. Fr. **105**: 37 (1958).
Chrysophyllum wilmsii Engl., Mon. Sapot. Afr.: 47 t. 16 (1904). Type: Transvaal *Wilms* 1812 (B†, holo.; K!).
Boivinella wilmsii (Engl.) Aubrév. & Pellegr. in Bull. Soc. bot. Fr. **105**: 37 (1958).

CITATION OF SPECIMENS

In the interests of uniformity contributors are requested to follow the recommendations of the Botanical Research Institute, Pretoria (Technical note: Gen. 4, Oct., 1967) by citing specimens according to the one degree grid system. Distribution data are given separately for each province and are arranged in the following sequences: South West Africa, Botswana, Transvaal, Orange Free State, Swaziland, Natal, Lesotho, Cape. Within each province degree squares are listed in numerical sequence, i.e., from west to east and from north to south. Whenever possible locality records should be given to within a quarter degree square. The collectors' names and numbers are underlined (printed in italics) to avoid confusion with the numbers of the degree squares, e.g.: NATAL—2829 (Harrismith): Cathedral Peak Forest Station (-CC), *Killick 1527* (PRE); . . . CAPE—3418 (Simonstown): Hottentots Holland mountains, Somerset Sneeukop (-BB), Nov., *Stokoe s.n.* sub. SAM *56390* (SAM).

REFERENCES

These should be given in the text as follows: Jones (1968) or (Jones, 1968) or, where reference to a specific page is required, Jones (1968:57) or (Jones, 1968:57). **Literature cited** should be arranged alphabetically by surnames, chronologically within each name, with suffixes a, b, etc., to the year for more than one paper by the same author in that year. Titles of **periodicals** must be abbreviated according to the *World List of Scientific Periodicals*, 4th ed., London: Butterworth or when unable to trace the title in this list (as will be the case in taxonomic papers where abbreviations of 18th and 19th century periodicals are required) the abbreviations given in *Botanico-Periodicum-Huntianum*, Pittsburgh: Hunt Botanical Library, 1968, should be followed. Periodical titles should be underlined once (for italics). If an author is unable to determine the correct abbreviation of a journal title he is advised to type it out in full and leave its abbreviation to the Editor. Titles of **books** should be underlined and given in full, together with the place of publication, name of the publisher and an indication of the edition if other than the first; e.g.:

Davis, P. H. and Heywood, V. H., 1963. *Principles of Angiosperm Taxonomy.* Edinburgh and London: Oliver and Boyd.
Riley, H. P., 1960. Chromosome numbers in the genus *Haworthia. Jl S. Afr. Bot.* **26**: 139—148.

Jl S. Afr. Bot. 37 (4): 249-266 (1971)

TWO NEW SPECIES OF *ALOE* (LILIACEAE) FROM SOUTH TROPICAL AFRICA

L. C. Leach

Abstract

Two new species of *Aloe* (*Liliaceae*) are described and their apparent relationships discussed as well as some aspects of the possible identity of *Aloe baumii* Engl. & Gilg. The positions of the new taxa in the "Key to the species" in Reynolds, *The Aloes of Tropical Africa and Madagascar* (1966), are also indicated.

Uittreksel

TWEE NUWE SPESIES VAN ALOE (LILIACEAE) VANAF SUID-TROPIESE AFRIKA.

Twee nuwe soorte Aloe (Liliaceae) word beskryf en hulle skynbare verwantskappe sowel as sekere aspekte van die moontlike identiteit van *Aloe baumii* Engl. & Gilg. word beskryf. Die posisie van die nuwe taksa in die sleutel tot die soorte van Reynolds "*The Aloes of Tropical Africa and Madagascar* (1966)", word ook aangedui.

Aloe esculenta Leach, sp. nov.

Aloe rubrolutea sensu Reynolds, Aloes S. Afr.: 327 (1950), pro parte quoad specim. *Hahn* s.n. in *Reynolds* 2423 et distrib. Ovamboland.—sensu R. Story, in Bot. Surv. S. Afr. Mem. **30:** 15 (1958).—sensu Jacobsen, Handb. Succ. Pl. **1:** 199 (1960), pro parte quoad distrib. Ovamboland.

Aloe littoralis sensu Reynolds, Aloes Trop. Afr. Madag.: 317 (1966), pro parte quoad specim. *Codd* 7157 et distrib. Barotseland et Ovamboland.

It also seems probable that this is the *A. baumii* referred to by Warburg, in his account of Baum's Kunene-Sambesi Expedition, as being common in the Humbe region.

A. littorali Bak. arcte affinis sed plantis acaulibus, saepe caespitosis et habitu frutescenti; rosulis parvioribus, foliis paucioribus; foliis maculis albidis grandibus copiose transverse valde notatis; inflorescentia ad medium laxe pauciramosa; bracteis plerumque grandioribus usque ad 27 mm longis; floribus subclavatis, stigmate usque ad 8 mm exserto differt.

Plantae acaules vel interdum caule crasso, brevi (usque ad 40 cm), saepe decumbenti, saepe caespitosae et habitu frutescenti. *Folia* c. 20, rosulata, 40—50 (60) cm longa, basi 7—8 (10,5) cm lata, gradatim decrescens versus apicem, plerumque patula, saepe recurva; *supra* basi plana, superne profunde canaliculata, grisea vel griseo-viridia interdum subroseo-brunnescentia, copiose albo-maculata, maculis lenticularibus irregulariter transverse notata; *subtus* valde convexa, plerumque spinarum atro-brunnearum acutarum serie mediana valde armata; *margines* leviter sinuato-dentati vel interstitiis rectis, dentibus brunneis

Accepted for publication 26th April, 1971.

Plants forming clumps near Ondangua, Ovamboland.

Plants in dense masses near Roçadas, S. Angola.

FIG. 1.
Aloe esculenta Leach.

acutis deltatis, 3—5 mm longis, 10—20 mm distantibus ferociter armati. *Inflorescentia* paniculata e medio laxe pauciramosa, 1—3 simultania, plerumque c. 1,5 m, raro usque ad 2,3 m alta; *pedunculo* basaliter plano-convexo deinde tereti; ramis 3—5, initio late patulis deinde plus minusve abrupte erectis, raro ramulosis; *racemis* plerumque 3—6, raro ad 9, anguste cylindrico-acuminatis, c. 6 cm diam., 30—40 cm longis, ubi fructicantibus usque ad 80 cm interdum elongatis. *Bracteae* ovatae acutae, tenues scariosae albidae, valde deflexae, 20—27 mm longae, 10—11 mm latae, 5 vel multinervatae. *Pedicelli* 5—6 mm longi. *Perianthium* initio coccineum demum flavescens, cylindrico-trigonum subclavatum, 28—30 mm longum, circum ovarium c. 6 mm diam. supra medium usque ad 8 mm amplificatum; *segmenta exteriora* per 15—18 mm libera, 7-nervata, nervis 3 longioribus ad apicem congestis; *segmenta interiora* latiora, obtusiora, nervis 3 prominentibus confluentibus, carinam obtusam formantibus; marginibus latis, albido-translucentibus. *Filamenta* albida; *antheris* usque ad 6 mm demum exsertis. *Ovarium* c. 7 mm longum, 3 mm diam; *stylus* pallide stramineus; *stigmate* usque ad 8 mm demum exserto. *Semina* atro-brunnea, ala membranacea albido-translucenti, atro-punctata, 7,5—12 mm longa, 4—5 mm lata.

Typus: Angola, Huila Distr., *Leach & Cannell 13818* (BM; LISC; PRE, Holo.; SRGH).

ANGOLA: Huila Distr., Pereira d'Eça, alt. c. 1 000 m, fl. 7.viii. 1967, *Leach & Cannell 13818* (BM; LISC; PRE; SRGH).

ZAMBIA: Barotseland, ±24 km S. of Nangweshi, *Codd* 7157 (PRE).

S.W. AFRICA:—1715 (Ondangua); ± 16 km S. of Ochikango (-DB), fl. 7. viii. 1967, *Leach & Cannell 13817* (PRE); Ondangua, open sandy flats with scrub mopane (-DD), Hort. Windhoek, fl. July 1961, *Giess & De Winter 2159* (PRE); ±16 km N. of Ondangua (-DD), fl. 23.vii. 1965, *Leach, R. D. & E. Bayliss 13037* (K; M; SRGH; WIND).
1820 (Tarikora); Nama Pan (-DC), fl. 7.viii. 1955, *Story 5135* (PRE).
1821 (Andara); Caprivi Strip, Andara (-AB), 1968, *S. Roux* s.n. (PRE).
Without precise locality:
"N. Ovamboland near the Kunene River", cult. & fl. Johannesburg, 18.viii.1941, cum photo., *Hahn* s.n. hort. *Reynolds 2423* (PRE);
"Kaokoveld Native Reserve", *Dr. S. Thompson* s.n. (PRE).

BOTSWANA: 1821 (Andara); Old Mohembo (-BD), cult. & fl. Nelspruit, 11.vii.1964, comm. *Mockford*, hort. *Leach 12294* (PRE).

The category to which this taxon should be assigned has provoked much thought and discussion; although quite distinct, it is obviously closely related to *A. littoralis* (syn. *A. rubrolutea* Schinz) of which it could perhaps be considered to be an ecologically separated subspecies. However the extent and constancy of the differences, reinforced as they are by the extensive but apparently discrete distribution of the vast numbers of plants involved and considered against the

background of the characters used in the present classification of the genus, have finally persuaded the writer that this newly described taxon should be accorded specific rank. It is in any event not considered to be opportune to introduce subspecific rank at this stage of our knowledge of the genus, and particularly of the group of which *A. littoralis* and *A. esculenta* are members.

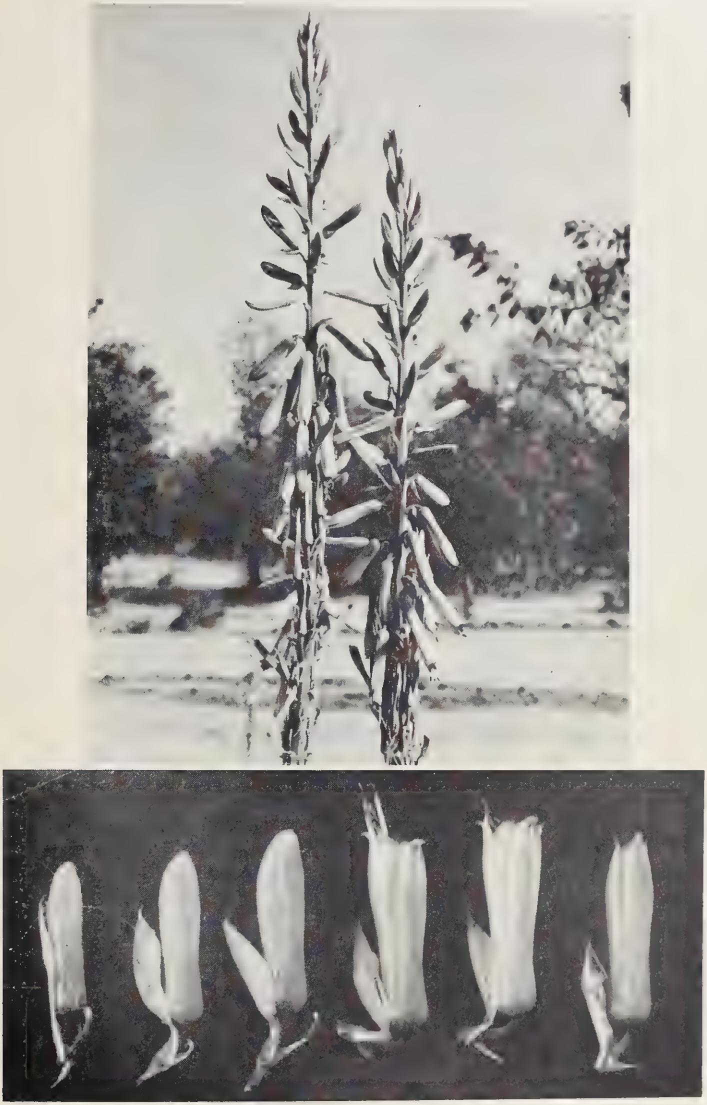
In common with most species in this difficult genus the extent of variability of such characters as leaf markings, size of bracts, pedicel and perianth length, extent to which anthers and style are exserted etc. is such that it may sometimes be found to be extremely difficult to differentiate between herbarium specimens of *A. littoralis* and *A. esculenta* when there is no indication of habit or of the branching of the inflorescence; however, when these details are known, or in the field, it is considered that no difficulty should be experienced.

The most obvious difference lies in the respective habits of the two species: *A. littoralis* is essentially a caulescent, simple stemmed, solitary plant, whereas the acaulescent *A. esculenta* is a gregarious species, frequently of shrubby habit and often forming clumps both by division of the rosettes after flowering and by offsets from the base. Individuals are also generally much smaller, with fewer, proportionally narrower leaves which are more spreading recurved than those of *A. littoralis*.

The leaves of the new species are copiously white-spotted, with the large conspicuous spots arranged in transverse wavy bands; the leaves of *A. littoralis* are also sometimes white-spotted, particularly when young, but never as conspicuously as those of its relative.

A few thorns are occasionally found on the median line towards the apex, on the underside of the leaves of *A. littoralis*, these also being mostly restricted to young plants, but in *A. esculenta* a similar line of strong thorns appears always to be present and to extend for about two-thirds the length of the leaves which are also sometimes sharply keeled along the same line.

The inflorescence of *A. esculenta* is a laxly, 3—5 (7) branched, open panicle, branched from about the middle with initially widely spreading, mostly simple branches, so that the usual number of racemes is 3—6 (the maximum counted being 9). The inflorescence of *A. littoralis*, however, is usually branched low down with more numerous less widely spreading branches, the lower of which are generally rebranched, so that there may be 20 or more closely set racemes to one inflorescence. A young plant of this latter species from the Sabi valley in Rhodesia, cultivated in Salisbury and flowering in May/June 1970 bore an inflorescence with 12 branches and 24 racemes. The length of the racemes appears to be a somewhat variable character in both species although those of the new species seem generally to be longer and slightly less densely flowered.



Flowering racemes with subclavate flowers 1:1.
Leach & Cannell 13818, near Pereira d'Eça, S. Angola.

FIG. 2.
Aloe esculenta Leach.

The bracts of *A. esculenta* are larger than those of its relative, averaging 20 mm or more (up to 27 mm) in length as compared with 12—18 mm; however this character appears to be no more reliable in individual instances than it is generally in the genus, e.g. those of Story's plants from Nama Pan are comparable with those of *A. littoralis* while in the rather disjunct colony in Barotseland, represented by *Codd 7157* they average only $\pm$10—11 mm in length, other minor divergencies exhibited by these plants are considered to be no greater than is to be expected in such a widely separated population.

The perianth of the new species is distinctly subclavate, while that of *A. littoralis* is straight or almost so with the stigma seldom, if ever, more than 3 mm exserted against the 8—10 mm normal in *A. esculenta.*

There is also a difference in flowering periods and behaviour: the new species flowers regularly during July and August (both in the wild and in cultivation), while *A. littoralis* is very erratic in its flowering dates (sometimes flowering twice in a season), appearing to be influenced by rainfall far more than by season, although plants generally flower much earlier than does *A. esculenta.*

Finally, Story in *Botanical Survey S. Africa Mem.* 30: 15 (1958) remarks, of plants near Nama Pan, "the leaves were tasted raw and boiled and found to be juicy and not unpleasant." This rather unsuspected character does not however, appear to be entirely constant, as the bitter principle was occasionally found to be present in random samples from populations in Ovamboland and S. Angola in which it appeared normally to be absent. However, all leaves of *A. littoralis sens. str.* which were tasted were found to be extremely bitter.

The habitats of the two species are generally quite different: *A. esculenta* appears to be almost entirely restricted to the recent sandy soils of the flats of the inland drainage areas lying to the south and east of the Cunene river, mainly between the 16th and 18th parallels, on the Ovamboland plains and northwards to as far as Mupa in southern Angola.

A. littoralis sens. str. on the other hand seems to be usually, if not entirely, associated with geologically older formations, and is distributed more or less on a broad arc from Luanda southwards to Windhoek and beyond, thence sporadically across the continent to its most easterly known station, in Moçambique near the Limpopo river some few miles from Pafuri.

Plants of *A. esculenta* attain their maximum size around Ondangua in Ovamboland, where they occur in open situations, usually in association with *Hyphaene*. In this area division of the rosettes and production of offsets is far more frequent than elsewhere, this, as well as the robust growth (plants occasionally develop a stout stem up to about 40 cm high), is thought probably to be due to more favourable conditions, particularly perhaps to the paucity of competition. As one proceeds northward, colonies of *A. esculenta* are seen, which although still densely populated and sometimes even outnumbering the dwarf

Plants from the disjunct population in Barotseland with typically subclavate flowers and far exserted stigma
L. E. Codd 7157, 23 July 1952.

FIG. 3.
Aloe esculenta Leach.

Photo by courtesy of:
Chief, Botanical Research
Institute, Pretoria.

"Mopane" among which they frequently occur, tend to become smaller and less frequent and the plants generally smaller and more often solitary. The main distribution of this species appears to be terminated much more abruptly toward its southern limits, plants being plentiful in the Ondangua region but seen for only about 25 miles along the road to Namutoni. Near Namutoni a few typically tall-stemmed specimens of *A. littoralis* were seen and this is possibly the nearest approach made by the two distributions.

Such variations as occur seem to be restricted to the disjunct populations which occur around the outer limits of the distribution, such as those previously

mentioned, in which leaves are more erect and the bracts much smaller than in typical populations, and another at Mohembo in NW Botswana near the Caprivi Strip, in which both leaves and branches of the inflorescence are less widely spreading than is normal for the species. Plants at this latter locality appear to have been cultivated in the vicinity of the old police post, but from the records from other not too distant localities it seems quite possible that they were originally indigenous in the area.

It is considered that the foregoing and other minor variations are of no importance in the general context of a genus which normally accommodates such a great extent of variation within accepted specific limits.

Acaulescent plants are also reported from the western end of the Etosha Pan but I have not seen these (nor any herbarium material) and they are not included here. Mr. W. Giess, writing in *Dinteria* 5 (1970) records that although only acaulescent plants are to be found in this region today, it is only recently (at least as recently as 1957) that tall, simple stemmed, typical *A. littoralis* was plentiful.

It seems advisable therefore that a decision regarding these plants and those from Pungo Andongo and elsewhere in Angola, referred to by Reynolds, should be left in abeyance pending further investigation.

Aloe esculenta would "key out" in *Reynolds, The Aloes of Tropical Africa and Madagascar:* 118 (1966) to 56a in:—

Group 9. Mostly series *Verae* Berger emend. Reynolds
  2. Perianth glabrous
    B. Inflorescence over 1 m tall
      (a) Inflorescence simple or few branched

56 *A. metallica*	57 *A. massawana*	59 *A. officinalis*
56a *A. esculenta*	58 *A. vacillans*	59a *A. officinalis* var. *angustifolia*

Appearing to be closest to *A. metallica* Engler & Gilg among these taxa, it is distinguished therefrom by its frequent habit of forming groups from basal offshoots and division of the rosettes; by its generally longer, proportionally narrower spreading leaves which are copiously large white-spotted and armed with strong thorns on the median line underneath; by its more freely branched inflorescence and subclavate flowers with the stigma at length exserted up to 8 mm.

Plants acaulescent or sometimes with a short (up to 40 cm), stout, often decumbent stem; frequently of shrubby habit from division of the rosettes after flowering, sometimes forming clumps by this means when stems are decumbent, or less frequently by offshoots from the base. *Leaves* about 20, rosulate, 40—50 (60) cm long, 7—8 (10,5) cm broad at the base, gradually narrowing to an acute apex, mostly spreading, often recurved; *upper surface* flat low down,

Plant from Old Mohembo, Botswana, flowering at Nelspruit, 17 Aug. 1965. Flowers 1 : 1.

Fig. 4.

Aloe esculenta Leach.

Photos by courtesy of:
the late Dr. G. W. Reynolds.

becoming deeply canaliculate above, grey or grey-green to pinkish brown, copiously white-spotted, with the lenticular spots irregularly arranged in more or less transverse wavy bands; *lower surface* convex, strongly so towards the apex, similar in colour to the upper but more copiously spotted, usually armed with a line of strong, sharp, blackish brown thorns arising from white tuberculate bases on the median line for about half to two-thirds of the length of the leaf, often sharply keeled; *margins* slightly sinuate-dentate or with the interspaces straight, armed with sharp, shiny brown, deltate teeth, 3—5 mm long, 10—20 mm apart. *Inflorescence* a laxly 3—5 branched panicle, with the peduncle basally plano-convex becoming terete above, 1—3 simultaneously from a rosette, averaging 1,5 m tall, exceptionally up to 2,2 m, branched from about the middle with the branches usually initially widely spreading, becoming rather abruptly erect, very sparingly rebranched, so that the inflorescence has generally 3—6 racemes (9 being the maximum counted). *Racemes* narrowly cylindric-acuminate, ± 6 cm diam., 30—40 cm long, sometimes lengthening in fruit to about 80 cm. *Bracts* ovate acute, thin scarious whitish, strongly deflexed, 20—27 mm long, 10—11 mm wide when flattened, 5 to many nerved. *Pedicels* 5—6 mm long, lengthening in fruit to $\pm 12{,}5$ mm. *Perianth* deep pink, buds grey-tipped, open flowers cream or pale yellow striped, becoming more yellowish with age, cylindric-trigonous, subclavate, 28—30 mm long, ± 6 mm diam. across the ovary, enlarging to ± 8 mm above the middle; *outer segments* free for 15—18 mm, 7-nerved, with the 3 central longer, more distinct and confluent at the apex, with a pale yellowish border; *inner segments* broader and more obtuse than the outer, with 3 prominent confluent nerves forming a deep pink obtuse keel, with broad translucent whitish borders. *Filaments* whitish, filiform-flattened, the three inner narrower and lengthening before the outer, with the anthers in turn exserted up to ± 6 mm. *Ovary* 6-grooved ± 7 mm long, 3 mm diam. towards the base, narrowing to $\pm 2{,}5$ mm towards the apex; *style* pale straw coloured with the stigma at length exserted ± 8 mm. *Capsule* somewhat obtusely trigonous, $\pm$ oblong-ellipsoid, ± 26 mm $\times$ 15 mm when almost ripe. *Seeds* dark brown, minutely sparingly tuberculate, with a broad, black speckled, translucent whitish membraneous wing, orange-tinged around the seed, 7,5—12 mm long, 4—5 mm broad, usually simple, sometimes with a slight keel or smaller wing set at right-angles to the main wing.

There is a strong possibility that this taxon could be the *Aloe baumii* Engler & Gilg, which Berger included in the synonymy of *A. zebrina* Bak.; this synonymy was subsequently accepted by Reynolds, apparently on the evidence of the photograph of plants at the Kubango River (Warburg, Kunene-Sambesi Exped.: t.90, 1903) which purports to be of *Baum* 275 (the type of *A. baumii*) and which certainly appears to represent *A. zebrina.* However, the description by Engler & Gilg appears to differ from that of *A. zebrina* and from the photo-

graph in several details, e.g. "Floribus flavido-rubescentibus" and "tepalis lancolato-linearibus" would seem to fit the flowers of *A. esculenta* rather than of *A. zebrina* while "Paniculae ramis ut videtur a basi usque ad apicem dense florigeris" could scarcely be applied to the laxly flowered racemes of the latter species; furthermore there is no mention in the description of a basally inflated perianth. It is also stated in the narrative that plants are common from the Serra de Chella to beyond Cuito and that natives in the vicinity of Humbe (near Roçadas of today) made cakes of the "Blumen", "Bluten" and "Blattern", scarcely practicable with *A. zebrina* which is relatively scarce in this area while *A. esculenta* occurs in thousands in densely populated colonies. Story in Botanical Survey S. Africa Mem. 30: 15 (1958) mentions that *A. rubrolutea* Schinz occurred near Nama Pan with "a habit similar to that of *A. zebrina*" and "growing in patches of an acre or so," "among the hundreds of specimens seen there were none arborescent"; these plants are now included in the author's concept of *A. esculenta*. Plants were in full bloom in early August, and, perhaps most significantly "the flowers are stripped off the flowering stalk and pounded to make a spinach-like vegetable."

Various other references to the edibility of the flowers of *A. zebrina* appear all to arise from the description of this use by Warburg *l.c.* which it is considered can apply, in view of the circumstances outlined above, only to *A. esculenta* (*A. ?baumii*).

Berger in Gardener's Chronicle 35: 226 (1904) draws attention to some of the discrepancies between the description of *A. baumii* and plants in cultivation at La Mortola under that name, but finally, on the evidence of the apparent identity of those plants with the photograph in Warburg (*l.c.*), considered *A. baumii* to be synonymous with *A. zebrina*.

It seems probable from the foregoing that Berger's plants were, in fact, different from that of Engler & Gilg. However, as it has not been possible to locate a specimen of *Baum* 275, it appears to be advisable to accept the photograph as representing *A. baumii*, as previous authors have done, until concrete evidence to the contrary is forthcoming.

A puzzling circumstance is that the flowering date of *Baum* 275 is given as October, a date which does not coincide with any of the recorded flowering times of either species.

Aloe inamara Leach, sp. nov.

A. veseyi Reynolds affinis sed racemis brevioribus; bracteis angustioribus tantum 1-nervatis (rarissime 2); pedicellis longissimis; floribus rubiginosis basaliter truncatis valde ampliatis, genitaliis vix vel haud exsertis; succo inamaro differt.

Plantae scopulis dependentes, interdum rosularum tegetes pendentes usque ad 3 m longas formantes; surculis e basi exilientibus caulibusque usque ad 2 m longis × c. 2 cm diam., superne pauciramosis tantum ad apicem foliatis, foliorum veterum reliquiis amplexicaulibus vestitis, internodiis c. 1 cm longis. *Succus* inamarus luteus. *Folia* plus minusve 9, rosulata, 45—60 (90) cm longa, basi c. 4—5 cm lata, valde patula, deorsum versus falcata, usque ad 1 cm crassa basin versus; *supra* plana vel leviter concava prope basin, superne plana vel

Photo: L. C. Leach

FIG. 5.
The type locality of *Aloe inamara* Leach, Quicombo River mouth.

saepe convexa, pallidula flavovirentes (in apricis brunnescentes) obscure subtiliter lineata, maculis H-formibus pauci- vel numerosi-maculata, interdum fere immaculata; *subtus* convexa, pallidiora copiosius maculata, maculis plus minusve fasciata; *margines* aliquam translucentes cartilaginei, albidi vel subrosei, dentibus albidis, saepe apice brunneis, deltatis vel leviter uncinatis, 0,3—1 mm longis, irregulariter 4—20 mm distantibus; interstitiis leviter concavis basin versus, superne plus minusve rectis. *Inflorescentia* pendula paniculata, 40—55 cm longa, supra medium 4—6 ramosa; racemis arcuato-ascendentibus; *pedunculus* 30—45 cm longus, basi c. 7 mm latus, leviter biconvexus, superne teres, c. 5 mm diam., obscure striatulatus, e viridi brunneus, glabrus. *Racemi* breviter cylindraceo-conici vel fere subcapitati, racemo terminali c. 7,5 cm longo, c. 7,5 cm diam.,

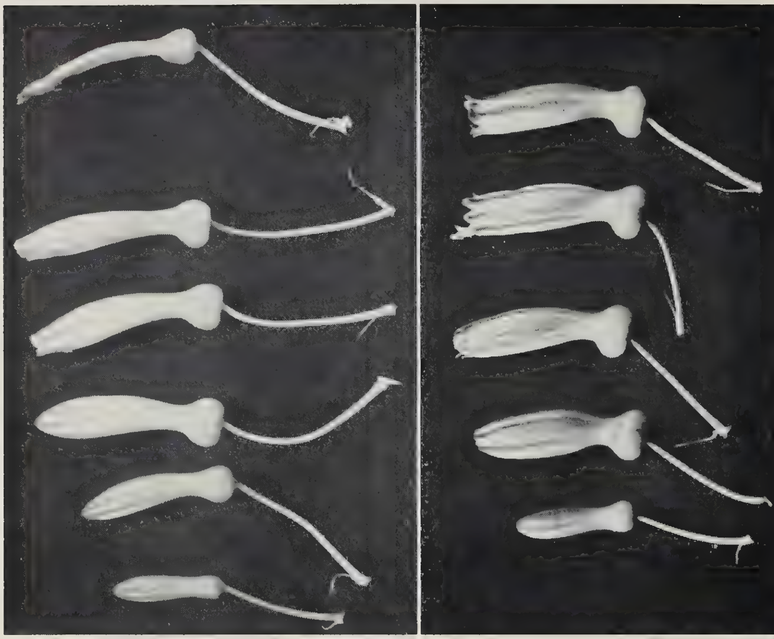
Photo: I. C. Cannell

FIG. 6.

The type plant of *Aloe inamara* Leach, flowering in habitat.

laterali breviore, pedicellis, gemmis floribusque valde patulis floribus apertis nutantibus; coma apicali parvula albida bractearum sterilium instructi. *Bracteae* triangulares attenuatae 7,5—9 mm longae, c. 3 mm latae, albidae scariosae, nervo uno atro-brunneo conspicuo praeditae. *Pedicelli* 22—27 mm longi. *Perianthium* rubiginosum, ad apicem viridulum, 26—29 mm longum, obtuse trigonum, leviter decurvatum, basi truncatum valde ampliatum ad 8 mm diam. inde abrupte constrictum, apicem versus gradatim ampliatum ad c. 7 mm diam., denuo angustatum, ore aperto c. 6 mm diam.; *segmenta exteriora* per 6,5—8 mm libera, nervis 3 brunneis ad apicem confluentibus et nervis 2 lateralibus brevioribus obscurioribus; *segmenta interiora* latiora nervis 3 confluentibus,

marginibus translucentibus latissimis albidis. *Filamenta* albida, superne dilute virescentia; *antheris* vix vel haud exsertis. *Ovarium* pallide viride, c. 5,5 mm longum, c. 2,5 mm diam., 6-sulcatum; *stylo* basi luteo superne virescenti; *stigmate* albido, vix vel haud exserto.



Photos: L. C. Leach

FIG. 7.
Flowers 1/1 approx. Showing variation in shape.

Typus: Angola, Cuanza-Sul, *Leach & Cannell 14608* (LISC, holo.; PRE).

ANGOLA: Cuanza-Sul Distr., fluvii Quicombo ad orem scopulis dependentes, fl. 11.x.1970, *Leach & Cannell 14608* (LISC; PRE); ibidem Hort. Leach., fl. Nelspruit, 15. xi.1968, *Leach & Cannell 13938* (BM).

With obscurely lineate leaves with whitish H-shaped spots and flowers with a much inflated truncate base, *A. inamara* clearly belongs in series *Saponariae* Berger, in which, in leaf markings and texture as well as flowers with long pedicels and relatively small bracts, its nearest relative appears to be the much larger and otherwise quite distinct *A. swynnertonii* Rendle. However, in many respects the new species appears to be more closely related morphologically to *A. veseyi* Reynolds from Kalambo Falls near the southern end of Lake

Tanganyika, and an as yet undescribed taxon from the Kambole Escarpment, also in north-eastern Zambia; these, in habit, inflorescence and particularly in falcately curved leaves, display a quite remarkably close similarity with *A. inamara*. The trio appears possibly to comprise a most interesting evolutionary

Photos: L. C. Leach

Variation in leaf markings. Inflorescence.

FIG. 8.
Aloe inamara Leach.

situation in which it seems that development may have been either divergent or convergent. In this connection it may be noteworthy that a somewhat similar situation occurs in *Euphorbia* in which the western Angolan *E. dekindtii* Pax, *E. atrocarmesina* Leach and *E. semperflorens* Leach are closely related to *E. williamsonii* Leach from north-eastern Zambia, while the very similar distributional link which is evident in *Monadenium* follows an almost identical path from Tchivinguiro and Mount Moco in western Angola to Mbala (Abercorn) in north-eastern Zambia.

The new species differs from both of the Zambian taxa in having a much inflated truncate base to the perianth, much longer pedicels and, it seems, the complete absence of the bitter principle in the sap, which on the evidence of taste appears to be plentifully present in both the related taxa. *A. inamara* differs additionally from *A. veseyi* in its shorter, sometimes almost subcapitate racemes

Photo: I. C. Cannell Photo: L. C. Leach

Fig. 9.

Aloe inamara at the type locality.

of red flowers, narrower 1-nerved bracts and scarcely or not at all exserted genitalia, and from the Kambole plants in its obscurely lineate, H-spotted leaves which contrast quite sharply with the unmarked grey-green leaves of the undescribed taxon, the flowers of which are markedly trigonously indented after the manner of those from plants in the *A. chabaudii* Schonl. relationship.

A. inamara was found growing on the almost vertical cliffs at the mouth of the Quicombo River, about 10 km south of Novo Redondo; plants are plentiful but grow mostly in quite inaccessible situations; it was consequently not possible to obtain more than the two flowering specimens of the type material.

The species appears to be tolerant of either full sun (leaves then becoming brown) or heavy shade; plants seem to flower rather reluctantly under either condition, although apparently over an extended period.

Plants hanging on cliff faces, with offshoots from the base and stems up to 2 m long × about 2 cm diam., sparingly branched above, foliate only towards the apex, clothed with the dry amplexicaul remains of old leaves, with the internodes about 1 cm long, sometimes forming pendent mats of rosettes up to 3 m long. *Leaves* about 9, rosulate, 45—60 (exceptionally up to 90) cm long, 4—5 cm wide towards the base, widely spreading, falcately curved with their apices pointing downwards, up to 1 cm thick towards the base; *sap* yellow, lacking the usual bitter principle; *upper surface* flat or slightly concave towards the base, becoming more turgid and often convex towards the apex, or in older leaves often with the apex brown and shrivelled, pale yellowish green (brown when exposed to the sun), obscurely finely lineate with few to numerous, small, more or less H-shaped whitish spots (sometimes almost immaculate); *lower surface* convex, paler and more copiously spotted than the upper, with the spots arranged in more or less transverse wavy lines; *margins* somewhat translucent cartilaginous, whitish or faintly pink, armed with whitish, often brown tipped, deltate or slightly hooked teeth, 0,3—1 mm long, irregularly spaced, 4—20 mm apart, with the interspaces slightly concave low down, becoming straight above. *Inflorescence* a 4—6 branched pendulous panicle 40—55 cm long, upturned towards the apex with arcuate ascending racemes; peduncle 30—45 cm long, ±7 mm wide at the slightly biconvex base, terete above, about 5 mm diam., slender and wiry, obscurely striatulate, greenish brown, glabrous, with only a trace of bloom. *Racemes* sublaxly flowered, shortly cylindric-conical to almost subcapitate, the terminal about 7,5 cm long × 7,5 cm diam., the laterals shorter; pedicels, buds and flowers widely spreading, the open flowers becoming nutant; with a small whitish coma of sterile bracts at the apex. *Bracts* triangular attenuate, 7,5—9 mm long, ±3 mm wide at the base, thin scarious whitish with a blackish brown nerve, rarely with an additional less conspicuous brown nerve to one side; those subtending the lower branches of the inflorescence rather inconspicuous, ±5 mm long. *Pedicels* 22—27 mm long, the colour of the perianth, minutely white flecked. *Perianth* dull red, greenish at the apex, becoming somewhat yellowish in open flowers, minutely white flecked in bud, 26—29 mm long, slightly decurved, much inflated at the truncate, somewhat obtusely triangular base, about 8 mm diam. across the ovary, abruptly constricted to about 7 mm, again narrowing to ±6,0 mm at the open mouth; *outer segments* free for 6,5—8 mm, very slightly spreading at the apex, with paler coloured margins and 5 brownish nerves, the three central confluent at the apex and the two lateral shorter and somewhat obscure; *inner segments* wider than the outer, with wide translucent whitish margins and

3 confluent dark nerves. *Filaments* whitish at the base, pale green above, filiform flattened with the anthers not or only rarely slightly exserted. *Ovary* pale green, 5,5 mm long, more or less cylindric, $\pm 2{,}5$ mm diam. towards the base, tapering very slightly to ± 2 mm diam. at the apex, 6-grooved; *style* yellow towards the base becoming greenish above; *stigma* white, scarcely or not exserted.

Aloe inamara would fit into the key in *Reynolds, The Aloes of Tropical Africa and Madagascar* (1966) under:—

Group 10. Plants pendent or semi-pendent,

and is distinguished from all others in this group by its longer pedicels and flowers with a much inflated truncate base.

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AN UNDESCRIBED NERINE FROM THE S.E. TRANSVAAL

Gordon McNeil

Abstract

A Nerine previously confused with the species *N. angustifolia* Baker and *N. appendiculata* Baker is described.

Uittreksel

'N ONBESKRYFTE NERINE VAN DIE S.O. TRANSVAAL.
'n Nerine vroeër verwar met die spesies *N. angustifolia* Baker en *N. appendiculata* Baker word beskryf.

Nerine platypetala McNeil, sp. nov.

Bulbus ovatus, 3 cm longus, 2 cm diam., collum varium; *tunicae* tenuissimae albae; *foliae* 3—5 glabrae, angustissime lanceolatae, ad 65 cm longae, sulcatae, ad apicem attenuantes et planae evadentes et obtusae terminanter, 2 mm latae, basi rubescentes 5 mm latae, spiraliter 1—2 vice tortiles; *pedunculus* teres, glabratus, robustus, sufflavus viridis, 40 cm longus, basi 6 mm diam. ad 4 mm; *spathae valvae* pallidae roseae, membranes, lanceolatae, 2 cm longae ad 1 cm latae; *umbella* 12—15 florae; *pedicelli* pulli virides, dense pubescentes, 5 cm ad 1,5 cm longi, 1 mm diam.; *segmenta perianthii* paene regulares, quasi coruscantes, punicea, basi rubescentes cum prominente linea rubra supra, et cum linea virida infra, coniuncta per 8 mm postea patula plana evandentes 3,9 cm lata hac causa nomen aptum est, id est "platypetala", evadentes exteriores segmenta perianthii subacuta cum apicula alba promintente pubigera, interiores obtusa, 6 mm lata ad 2,4 cm longa; *filamenta* linearia declinata et fasiculata, basi forma palmula coniuncta corona minuta, et breviore dimidio quam perianto; *antherae* 2 mm longae purpureo brunneae; *stylus* filamentae aequilongus, roseum rubescens ad stigma; *stigma* minute 3-lobatum profunde rubrum; *ovarium* fulgens pubescens saturate purpureo brunneum.

Bulb ovoid, 3 cm long, 2 cm diam. with a neck varying in length; *tunics* thin, white; *leaves* 3—5, synanthus or may be hysteranthus, glabrous, deep green, of thin texture, very narrowly lanceolate, up to 65 cm long, channelled and tapering evenly to a flat obtuse apex 2 mm wide, the base 5 mm wide, reddened, and twisted once or twice; *peduncle* terete, glabrous, stout, light green, 40 cm long, 6 mm diam. tapering to 4 mm; *spathe valves*, pale pink,

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membranous, broadly lanceolate, 2 cm long, 1 cm wide; *umbel* 12—15 flowered; *pedicels*, dark green, densely glandular pubescent, 5 cm—1,5 cm long, 1 mm diam.; *perianth* almost symmetrical spreading in a regular flat funnel form to 3,9 cm across, hence the name "platypetala"; *perianth segments*, oblanceolate, pink, glittering, flushed rose-red at base with a prominent red central streak on basal half of upper side, and green streak on apical half of lower side, connivent for 8 mm; 2,4 cm long by 6 mm wide, the outer segments subacute with a prominent white-haired apiculus and the inner segments obtuse; *filaments* pale pink, declinate, half as long as the perianth, closely bunched, rising from a minute corona and widened to a palmate base 1 mm by 1 mm which is appendiculate for the segments of the outer whorl only; *anthers* dark purple brown, 3 mm long by 1 mm broad; *style* equal in length to the filaments, bright pink; *stigma* minutely three lobed, deep red; *ovary* shiny, minutely pubescent, dark purple-brown.

TRANSVAAL: 2729BB (Volksrust) 10 miles N. of Volksrust in vlei, 28th Feb. 1966. *G. McNeil 17*, (holotype NBG; isotypes PRE, GRA, NU, K, and BM): 2730AC (Vryheid): Wakkerstroom Feb. 1917, *H. W. Beeton 181* (SAM *12488*): Wakkerstroom Jan. 1967, *Mauve and Tölken 4521* (PRE).

The species is considered closest to *N. pancratioides* Baker in its almost regular perianth and flat segments, and to *N. angustifolia* Baker in its glabrous peduncle, pubescent pedicels and ovary and to both in its long narrow semi-terete leaves. It differs from the first in its much larger markedly rubescent perianth, its stouter much shorter peduncle carrying a lesser number of flowers, and its spreading pedicels where those of *N. pancratioides* are bunched and erect, nor does it have its filaments alternating with "bifid square scales" as described by Baker for *N. pancratioides* and observed by the writer in herbarium specimens of it.

It differs from *N. angustifolia* in its almost actinomorphic perianth, and its broader, flatter, shorter perianth segments which deepen basally to dark red where those of *N. angustifolia* are more uniformly pink, and narrow, crisped and recurving, often falcate and quite irregularly arranged.

The writer has examined a wide range of plants at both known localities and found the nerine consistent for all diagnostic characteristics, nor has he ever found a sign of deviate or intermediate forms amongst it, nor among adjacent populations of *N. angustifolia* Baker and *N. appendiculata* Baker.

ACKNOWLEDGEMENTS

Thanks for invaluable help and encouragement in letters received from Miss Barker of Kirstenbosch, from Robert Sealy of Kew, and from Mrs. Mauve of the Botanic Research Institute, Pretoria, are here acknowledged.

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ASPECTS OF CELLULAR GROWTH AND DEVELOPMENT IN *NICOTIANA TABACUM* TISSUE CULTURED *IN VITRO**

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Abstract

The growth and development of long, multicellular, branched pseudothalli from tobacco tissue segments grown on nutrient agar in the presence of 4,0 mg/l indoleacetic acid and 0,08 mg/l kinetin, was investigated. Pseudothalli growing from the upper surface of an explant are 3—4 mm high and consist of tubular, bulbous and papillate cells. Their development follows a more or less sequential pattern along horizontal and vertical axes. On the under-surface pseudothalli are associated with giant cells and filaments growing on or into the agar. Following root formation and development, numerous root hairs, some dilated and bulbous, are established in the agar, between pseudothalli, or even in the air space above the callus.

Uittreksel

ASPEKTE VAN DIE SELLULÊRE GROEI EN ONTWIKKELING VAN *NICOTIANA TABACUM* WEEFSEL WAT *IN VITRO* GEKWEEK IS.

Die groei en ontwikkeling van lang, multisellulêre, vertakte pseudotalli vanuit tabakweefsel-segmente wat op voedingsagar in die teenwoordigheid van 4,0 mg/l indoolasynsuur en 0,08 mg/l kinetien gekweek is, is ondersoek. Pseudotalli wat op die boonste oppervlak van 'n eksplant ontwikkel is 3—4 mm lank en bestaan uit buisagtige, bolvormige en papillêre selle. Hul ontwikkeling volg 'n min of meer sekwensiële patroon d.m.v. horisontale en vertikale vlakke. Op die onderkant van die eksplant is die pseudotalli met reusagtige selle en filamente wat òf op die agar òf net onderkant die oppervlakte van die agar groei, geassosieer. Na wortel-vorming ontwikkel menigvuldige wortelhare, sommige waarvan verrek en bolvormig is, in die agar, tussen die pseudotalli, of selfs in die lugruim bokant die eksplant.

Introduction

Gautheret (1966) has enumerated in detail on the various cellular types that are susceptible to dedifferentiation. We find it interesting, too, that whereas companion and parenchyma cells of the intraxylary phloem and xylem parenchyma of the medullary rays generally show a greater tendency to de-differentiate than the pith parenchyma of tobacco stem tissue, the result of dedifferentiation does not depend on the nature of the initial tissue. In tobacco, namely, the newly-formed callus produced by xylem parenchyma is the same as that produced by the parenchyma of the internal phloem bundles (Ellis and Bornman, 1970).

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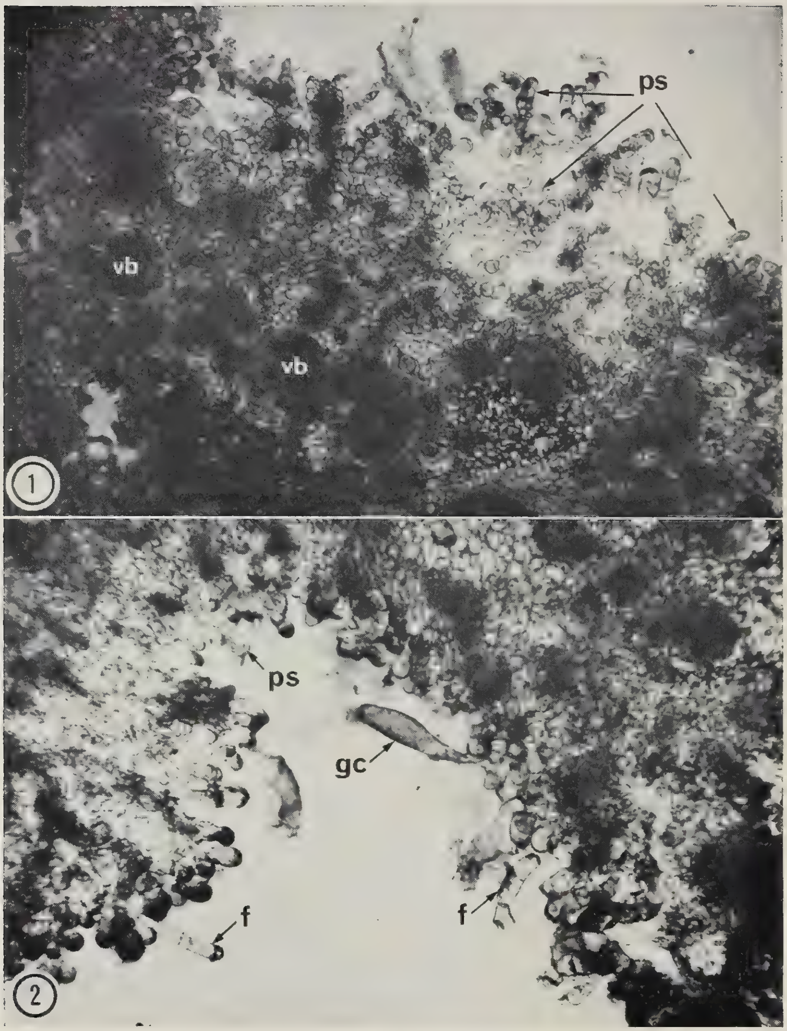


FIGS. 1–2.

Fresh tissue, polychrome stain, X36.—FIG. 1. Pseudothalli and vascular bundles on upper surface of explant.—FIG. 2. Loose, irregular callus on under-surface of explant.
f, filament; gc, giant cell; ps, pseudothalli; vb, vascular bundle.

It is commonly observed that a crystalline-like mass of callus becomes established from tobacco stem segments grown in the presence of levels of high auxin and low cytokinin and it appeared instructive to examine, in turn, those cell types which differentiate in response to the initial dedifferentiation of cells in the explant. Closer examination of such an explant's surface growth shows that it is made up of individual chains of cells, loosely packed together, giving the callus some resilience and a snowy to greenish-white appearance. The cells making up the chain appear to be in various stages of differentiation.

Materials and Methods

The conditions under which stem explants of *Nicotiana tabacum* cv. Kutsaga 614 were grown, were reported on in detail in a previous paper (Ellis and Bornman, 1970). All observations and measurements were made on fresh material, unstained or stained with aniline blue, polychrome, or safranin, or viewed under phase contrast. Since a feature of particular interest was the development of pseudothalli, this study was restricted to callus cultured on a basal medium in the presence of 4,0 mg/l indoleacetic acid (IAA) and 0,08 mg/l kinetin (CK).

Results and Discussion

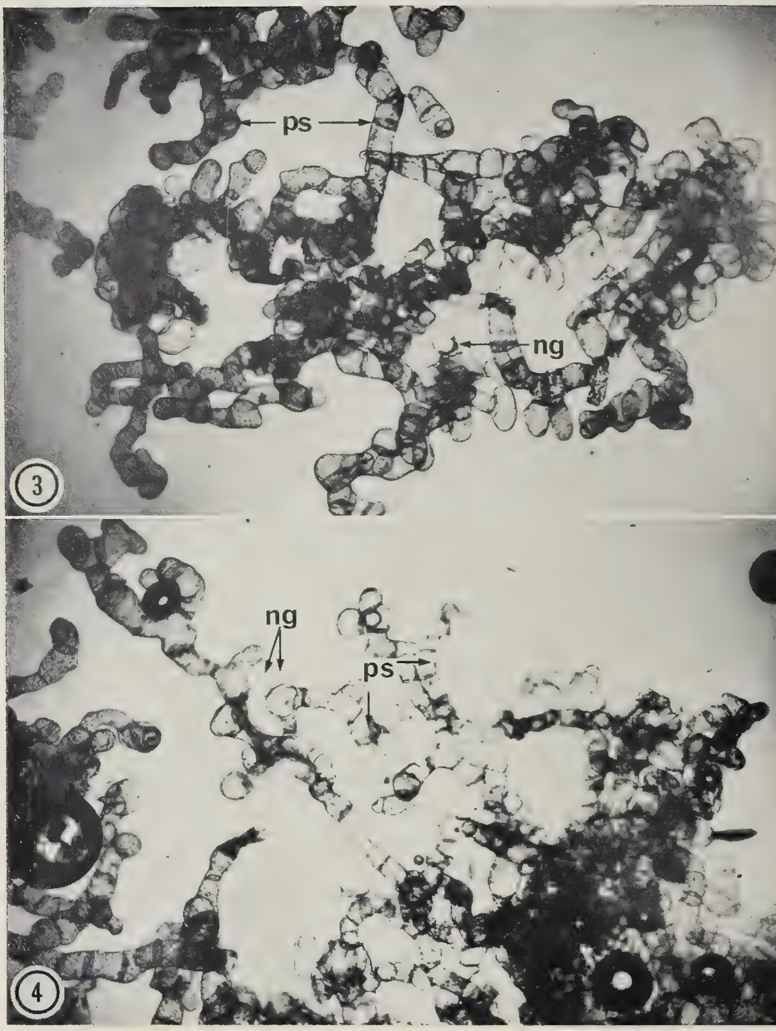
Characteristic of tobacco tissue cultured on nutrient agar in the presence of a high level of auxin, e.g. 4,0 mg/l IAA, is the development after four to five weeks of a mass of branched cellular filaments, the so-called pseudothalli of Gautheret (1957), giving it a downy or frosty appearance. There appears to be a distinct difference between supra-explant or aerial (Fig. 1) and sub-explant (Fig. 2) pseudothallial development.

Aerial pseudothalli

Pseudothalli developing on the upper surface of the stem explant into the air space above the agar, consist of multicellular, multibranched, rather loosely-knit chains (Figs. 3, 4). At their bases the pseudothalli are intergrown and dense, but toward their apices they are only loosely interconnected, if at all. In fact, most of the cells of a pseudothallus divide, grow, and develop in free air space. The individual filaments consist of approximately 20—30 and sometimes up to 40 cells, probably the upper limit in terms of osmotic absorption, and are from 3—4 mm high. Basically, pseudothalli are composed of four types of cells: tubular, bulbous or pear-shaped, papillate, and tracheary. The tracheary cells are discussed in a subsequent paper.

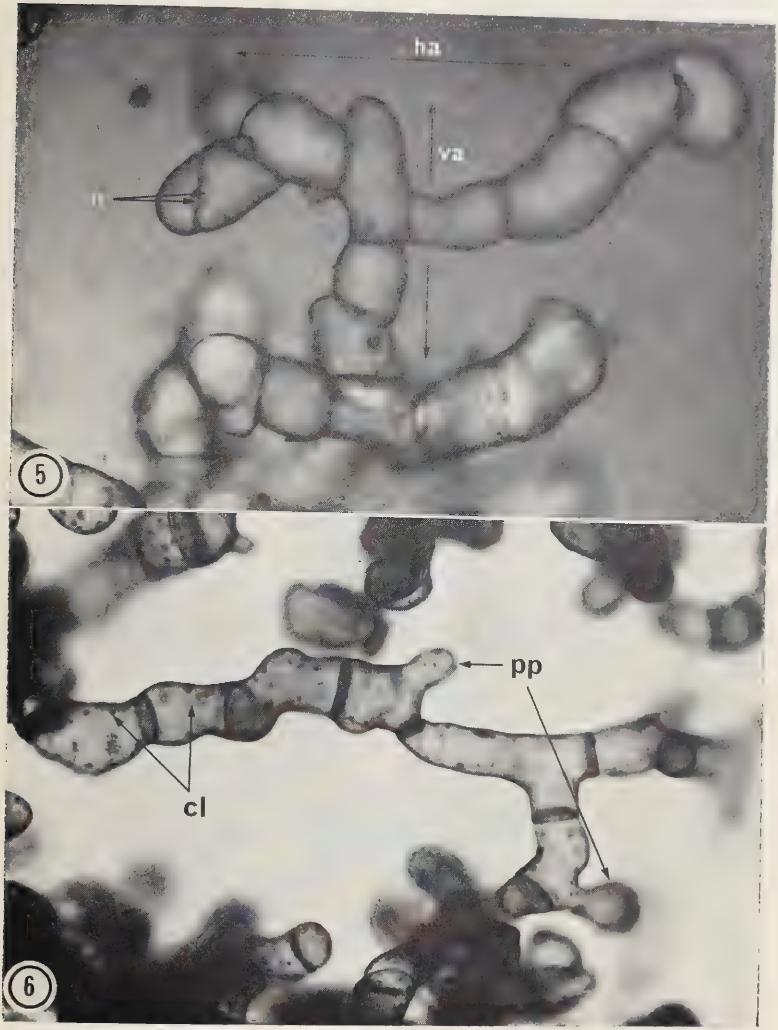
Tubular cells

The main body of the pseudothallus consists of long (up to 200 um) tubular cells, often with bulging protuberances. The younger division products are



FIGS. 3–4.

Fresh tissue, safranin, X60.—FIG. 3. Pseudothallial cells with numerous chloroplasts.—FIG. 4. Newly-budded cells devoid of chloroplasts.
ng, newly-budded cells; ps, pseudothalli.



Figs. 5–6.

Fresh tissue, aniline blue stain, X160.—Fig. 5. Pseudothallus showing development of vertical and horizontal axes.—Fig. 6. Pseudothallus showing protrusion divisions which ultimately will form columns of cells at right angles. Papillae clearly visible.
cl, chloroplast; ha, horizontal axis; va, vertical axis; n, nucleus; pp, papilla.

densely protoplasmic, exhibit active cyclosis, and have abundant mitochondria and undifferentiated plastids. The older cells, particularly those at the base, become increasingly vacuolate but contain numerous chloroplasts. The cell walls are thin and are speckled with pit-field-like depressions. The tubular cells display some anomalous features of division and growth, and a remarkable resemblance was found in respect of types of behaviour between these cells and those in free suspensions studied by Steward, Mapes and Smith (1958).

Stimulated by the plant hormones cytokinin and auxin, some cells on the surface of the original explant first divide to form a horizontal row of cells (Fig. 5). At a point along this axis, as a result either of periclinal division or of budding, vertical growth commences (Fig. 6) and after repeated divisions parallel to the short diameter of the cells, a vertical column of tubular cells is established constituting the main body of the developing pseudothallus. At some point on this vertical axis lateral development again occurs as a result either of anticlinal division or of budding. Thus, with the establishment of alternating horizontal and vertical axes, and also by inclined cell division (Fig. 9), S-, T- and Y-shaped—and multibranched variations of these—pseudothalli are formed. Not infrequently, the characteristic winglike appearance in a suspension culture (Steward *et al.*, 1958) of a mother cell flanked by two daughter cells, also is seen in aerial cellular development (Fig. 4).

Bulbous cells

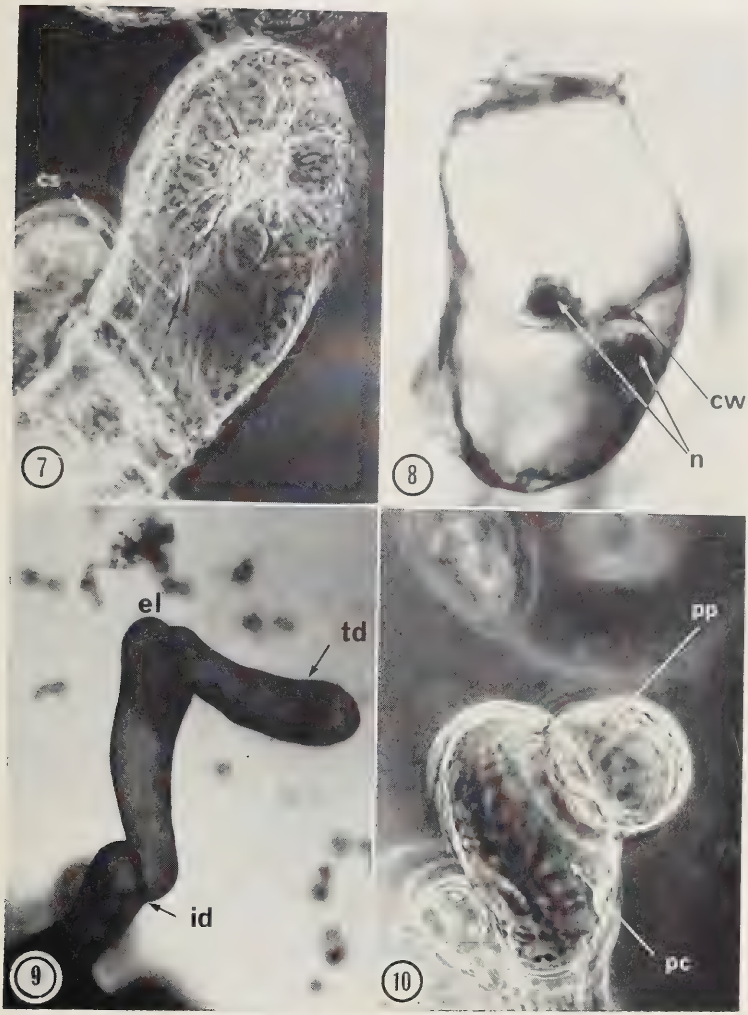
Terminal cells on the pseudothalli invariably are bulb, club or pear-shaped (Figs. 9, 10, 13, 14). Usually they are devoid of chloroplasts, hence the snowy appearance of such a culture colony, but the nuclei are large and protoplasmic streaming is active.

Papillate cells

On both tubular and terminal cells small protuberances or papillae often appear. These gradually enlarge although, initially at least, they remain constricted at the base (Figs. 6, 7). Papillae most likely are formed in response to a mitosis in the parent cell, part of whose increased volume of cytoplasm gradually pushes out into a bulge formed in a weakened area of the cell wall, probably a pit-field-like depression. Initially the papilla is a small, round cell, but once a mitotic nucleus has migrated into it, it enlarges, divides, and becomes tubular or, if in a terminal position, remains bulbous.

Sub-explant pseudothalli

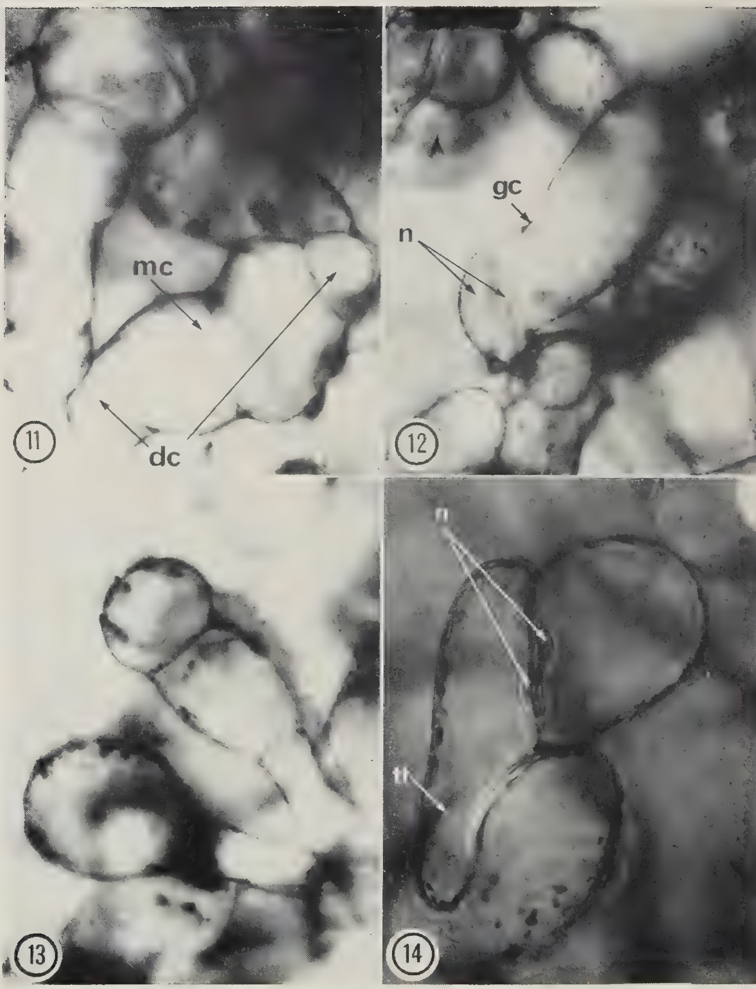
Pseudothalli on the undersurface of the stem explant are composed of short, dense cellular chains growing on, or slightly penetrating the agar surface. A feature of the sub-explant growth is the presence of giant cells and short filaments.



FIGS. 7–10.

FIG. 7. Phase contrast view of cell from superficial zone of parenchyma showing nucleus suspended by cytoplasmic strands, X45.—FIG. 8. Transverse division in a surface cell, aniline blue, X500.—FIG. 9. Pseudothallus showing transverse and inclined division as well as an elbow-like structure, polychrome stain, X160.—FIG. 10. Papillus developing from parent cell, phase contrast, X400.

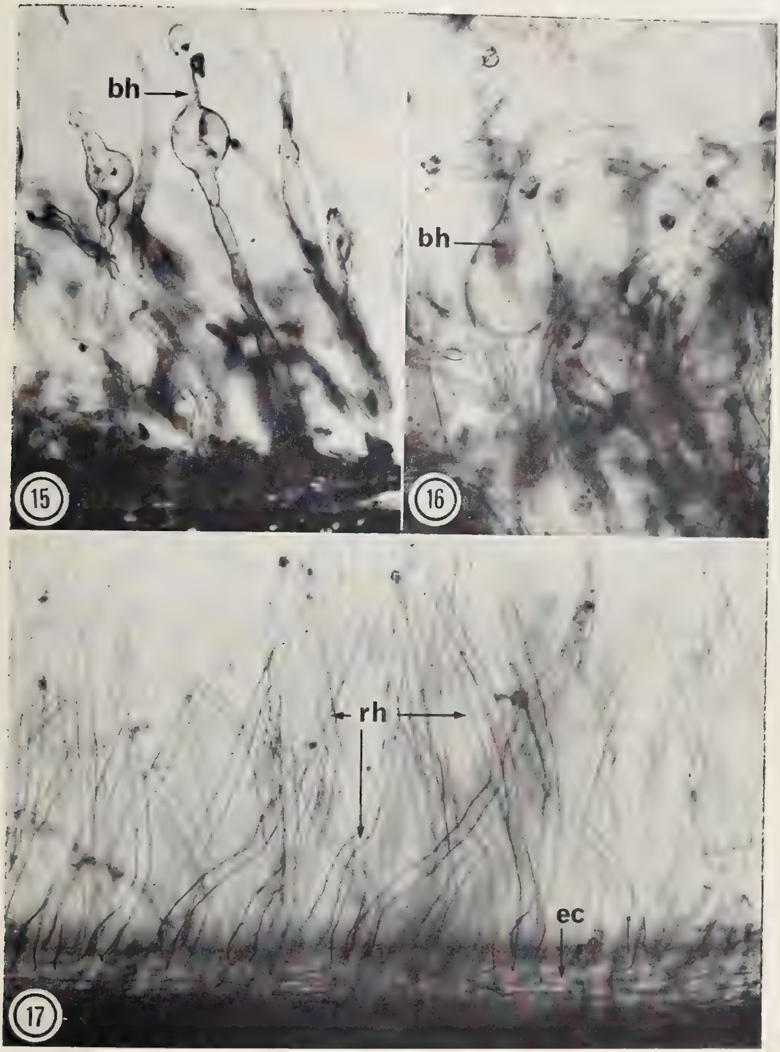
cs, cytoplasmic strands; cw, cell wall; el, elbow-like joint; id, inclined division; n, nucleus; pc, parent cell; pp, papillus; td, transverse division.



FIGS. 11–14.

Fresh tissue, aniline blue stain.—FIG. 11. Wing-like structures resulting from successive transverse divisions on opposite sides of mother cell, X160.—FIG. 12. Irregular cell divisions (arrows) of a giant cell, X140.—FIG. 13. Terminal transverse divisions of pseudothalli, X160.—FIG. 14. Recently divided cells in superficial parenchyma showing a tail-like extension often characteristic of a developing tracheid, X350.

dc, daughter cell; gc, giant cell; mc, mother cell; n, nucleus; tt, tail-like extension.



FIGS. 15–17.

Fresh mounts, aniline blue stain, X160.—FIG. 15. Root hairs with bulbous dilations growing in agar.—FIG. 16. Balloon-tipped root hair amongst pseudothalli.—FIG. 17. Aerial root hairs showing emergence from almost all epidermal cells.
ec, epidermal cells; bh, bulbous hair; rh, root hairs.

Giant cells

These are unusually large ($300\mu \times 100$—150 um), uninucleate cells (Figs. 2, 7, 8) with conspicuous cytoplasmic strands and are found only on the under-surface growing just above or in the agar. Giant cells appear to develop from the same type of surface cell which ultimately gives rise to a pseudothallus. Although highly vacuolated, giant cells divide, often forming daughter cells of unequal size. These divisions may continue until six or eight smaller cells occupy the original lumen of the giant cell. Steward *et al.* (1958) are of the opinion that the giant cells become polynucleate before internal divisions occur. The polynucleate conditions was not observed in the giant cells of our tobacco callus cultures.

Filaments

In freely suspended cell cultures unusually long, non-septate filamentous cells are often encountered. These have not be observed in tobacco tissue colonies but some cells, growing in close association with—or probably derived from—the giant cells, closely resemble them. Whether these filaments simply are the products of extension growth of the giant cells following wall formations in the latter, is not clear as yet. At least some filamentous growth can be traced back to large basal cells which are attached to giant cells and other surface cells by tail-like extensions (Fig. 14). Filaments are rarely composed of more than eight cells (Fig. 2) but could, as a result of division in various planes, probably give rise to branched pseudothalli.

Root hairs

With the attainment of equilibrium in pseudothallial development the larger proportion of growth in mass of the callus results from diffuse cambia which form immediately below the loose, irregular surface layers. Although isolated tracheary elements and islets of vascular tissue can be formed at the base of the surface pseudothallial layer, histogenic differentiation commonly occurs from the inner cells of the callus mass. Root primordia form and the developing roots course their way through the pseudothalli and grow into the nutrient agar or, not infrequently, exhibit negative geotropism and grow into the air space before curving back into the agar. Whether the root hairs develop in the agar (Fig. 15), in between the pseudothalli (Fig. 16), or in the air (Fig. 17), they are exceedingly numerous, each epidermal cell probably producing one. In the agar as well as in amongst the pseudothalli root hairs, up to 3 mm long, often exhibit huge, bulbous dilations.

Conclusion

The pseudothalli which develop in tobacco tissue in response particularly to a high auxin regime, consist of a number of different cell types in various

phases of maturation. Their development from surface cells which, in turn, are the products of dedifferentiation of xylem ray and intraxylary phloem parenchyma (Ellis and Bornman, 1970), appear to follow a regular and repetable sequence of stages. The final form is probably governed to a large-degree by the ratio and/or concentrations of the plant hormones auxin and cytokinin.

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Jl S. Afr. Bot. 37 (4): 281–289 (1971)

DIFFERENTIATION OF PSEUDOTHALLIAL TRACHEARY ELEMENTS IN *NICOTIANA TABACUM* TISSUE CULTURED *IN VITRO**

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Abstract

Under conditions of high auxin (4,0 mg/l indoleacetic acid) and low cytokinin (0,08 mg/l kinetin) tobacco stem explants grown *in vitro* on nutrient agar produce masses of aerial pseudothalli, some of the cells of which differentiate into tracheary elements. Secondary wall thickening in these differentiating cells may commence either simultaneously over the whole surface of the cell, progressively increasing in thickness, or with a localised deposition of wall material which then spreads in a circular or triangular manner, leading to a partial or total covering of the primary wall. The secondary thickening is mostly reticulate-pitted.

With extensive proliferation the pseudothalli intergrow and vascular islets become established from the peripheral cells of which roots may arise.

Uittreksel

DIFFERENSIASIE VAN PSEUDOTALLI TRAGEÏEDELEMENTE IN *NICOTIANA TABACUM* WEEFSEL WAT *IN VITRO* GEKWEEK IS.

Tabakstingel-eksplante wat *in vitro* op voedingsagar in die teenwoordigheid van hoë auksien (4,0 mg/1 indoolasynsuur) en lae sitokinien (0,08 mg/1 kinetien) gekweek word, produseer 'n massa pseudotalli, sommige van die selle waarvan differensieer om trageïedelemente te vorm. Sekondêre wandverdikking in dié differensiërende selle begin òf gelyktydig oor die hele selwand en verdik geleidelik òf met 'n gelokaliseerde neerslag van wandmateriaal wat dan op sirkulêre of driehoekige wyse versprei om uiteindelik die primêre wand gedeeltelik of geheel te oordek. Die sekondêre verdikking is meestal geretikuleerd gestippeld.

Met ekstensiewe vermeerdering groei die pseudotalli inmekaar en word vaatweefselnodules gevorm van die buitenste selle waarvan wortelprimordia ontstaan.

Introduction

Up to now, comparatively little attention has been paid to what appears to be the common occurrence of isolated tracheary cells in the superficial zones of callus on the aerial side of tobacco tissue grown *in vitro*.

Gautheret (1957) pointed out that tracheary differentiation could take place in an isolated cell. This almost casual reference is significant because it appears that it is with these single, isolated tracheids that the histogenesis of vascular nodules and strands—and thus possibly also roots—have their origin.

* This research was supported in part by the CSIR through a grant to the senior author and in part by the Department of Agricultural Technical Services. The photographic assistance of Mr. D. Tunnington, Department of Botany, is acknowledged.

† Present address: Botanical Research Institute, Pretoria.

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Steward, Mapes and Mears (1958) observed single tracheids but only in the central regions of their cultured material. However, we have consistently found tracheary cells differentiating in aerial pseudothalli, often even at the distal-most ends of these chains of connected cells growing into the air space. With repeated cell division and surface growth of the culture, the tracheary elements often become surrounded by parenchyma and eventually become organised into tracheary islets.

This study reports some of our observations on the origin and development of the single, pseudothallial-borne tracheary elements.

Materials and methods

The nutrient media, growth conditions, and preparation and culture of the tobacco (*Nicotiana tabacum*) tissue were reported in an earlier paper (Ellis and Bornman, 1970). Microscopic observations were made on fresh and macerated tissue as well as on scrapings of the callus surface, stained either with aniline blue or toluidine blue or safranin, or viewed under phase contrast.

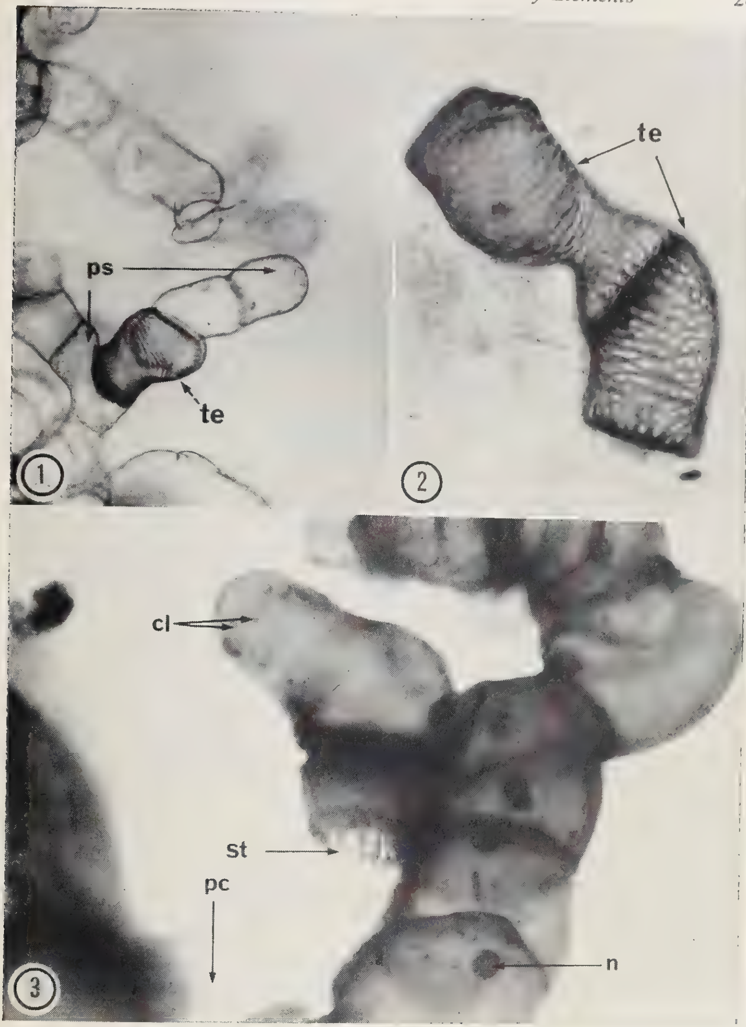
Particular attention was focused on tobacco callus cultured in the presence of 4,0 mg/l (high) indoleacetic acid and 0,08 mg/l (low kinetin).

Results and Discussion

Auxin and cytokinin, when incorporated in the culture medium in the ratio of 4,0 mg/l indoleacetic acid to 0,08 mg/l kinetin, produce a frosty growth of tissue, dense, compact and green at its base but loose and white at its acropetal surface. Closer examination shows that this pustular growth consists of innumerable pseudothalli made up of multi-branched chains of up to 20 or more cells.

Tracheary elements. Single, isolated tracheary elements are most commonly found near the bases of pseudothalli (Fig. 1) but also anywhere along the pseudothallus, particularly at branching points. Figure 2 shows two tracheary cells, the focal planes of which clearly indicate the zig-zag nature of a developing pseudothallial chain. In Fig. 3 vertical branching has occurred as a result of a number of cellular divisions, and in one of these cells the localised development of secondary wall thickening at a very early stage is apparent. Pseudothalli are frequently branched, producing Y-shaped, T-shaped or multiforked structures. Invariably, the parenchyma cells located at such a junction undergo secondary wall thickening and become tracheid-like in appearance. Figures 4–6 are of such an irregularly-shaped tracheary cell at different levels of focus and magnification, showing the areas of attachment to various adjoining parenchyma cells.

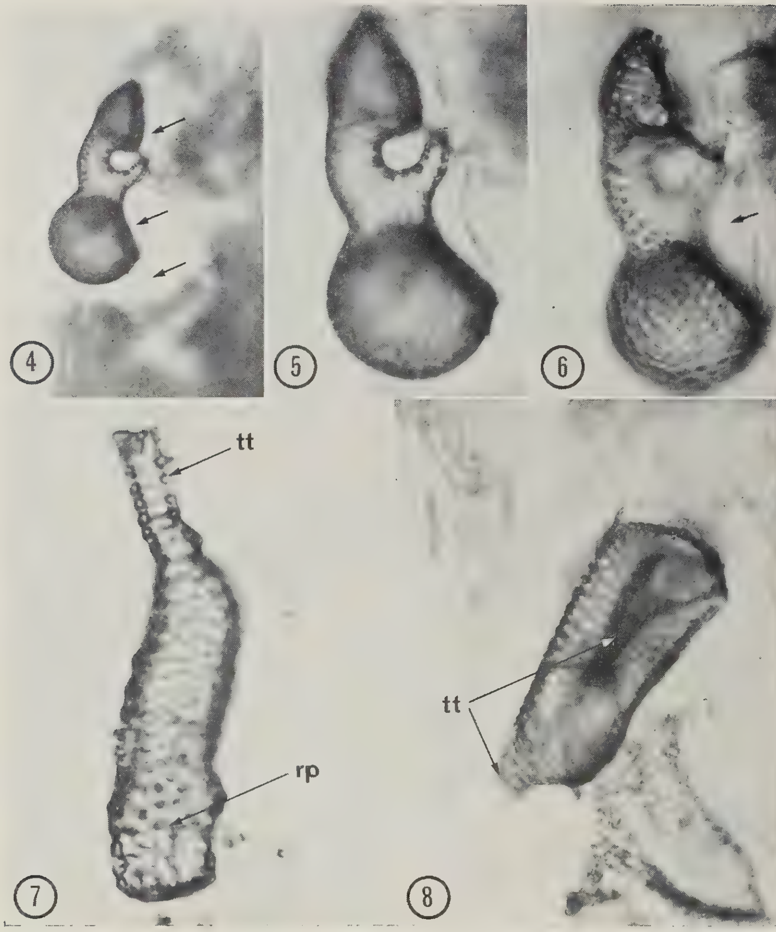
Large parenchyma cells, approximately 150 × 75um, differentiating into tracheary elements, often develop a characteristic tail-like structure (Fig. 7) which fits snugly into a corresponding depression in an adjoining tracheary element (Fig. 8).



FIGS. 1–3.

Tracheary elements from fresh and macerated tissue. Fig. 1. Single, isolated tracheary cell near the base of a branched pseudothallus, safranin, ×160. Fig. 2. Lignified, reticulate-pitted tracheary cells removed from macerated zig-zag chain of pseudothallial cells, toluidine blue, ×400. Fig. 3. Secondary wall thickening commencing in a parenchyma cell of pseudothallus, toluidine blue, ×400.

cl, chloroplast; n, nucleus; pc, parenchyma cell; ps, pseudothallus; st, secondary thickening; te, tracheary element.

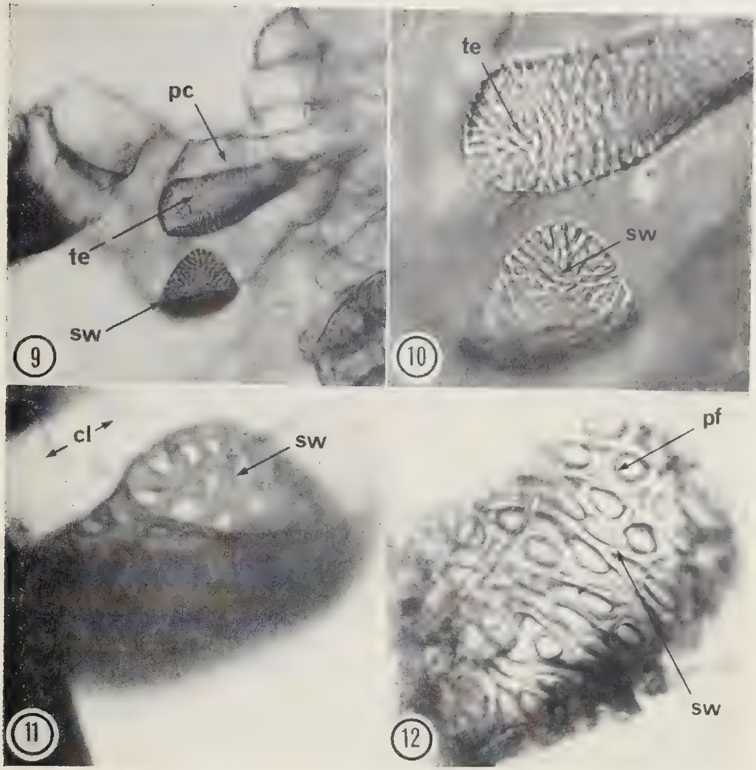


Figs. 4–8.

Macerated pseudothalli. Fig. 4. Unusually shaped tracheary cell, toluidine blue, ×160. Figs. 5–6. Higher magnifications of same showing surfaces where parenchyma cells were attached (arrows), ×400. Fig. 7. Reticulately-pitted tracheid with conspicuous tail, safranin, ×640. Fig. 8. Tracheary element with surface depression corresponding to fit tail from adjoining tracheary cell, safranin, ×400.

rp, reticulate-pitted; tt, tracheary tail

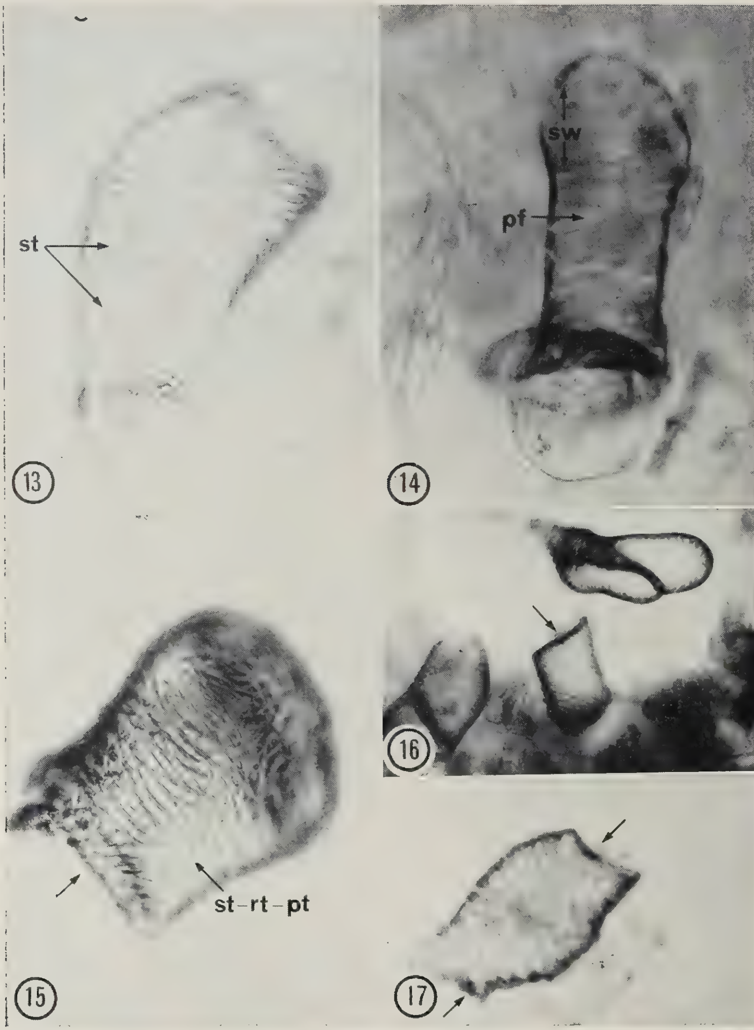
Deposition of secondary wall material. The secondary wall thickenings of these primary tracheary elements appear to be laid down in one of two ways. Firstly, and most interesting, a small area of primary wall becomes covered



FIGS. 9–12.

Fresh pseudothallial tissue. Fig. 9. Partial secondary thickening of walls of two adjacent tracheary cells, aniline blue, ×160. Fig. 10. Higher magnification of same showing nature of thickening which is reticulate-pitted, ×400. Fig. 11. Pitted secondary thickening of wall of cell still retaining chloroplasts, toluidine blue, ×640. Fig. 12. Outer surface of air-filled tracheid (resulting in clear definition) showing pitfields of primary wall overlain with strands of secondary thickening—evidence of exterior deposition of wall materials. safranin, ×1600. cl. chloroplast; pc. parenchyma cell; pf, primary pit field; sw, secondary wall; te, tracheary element

with secondary wall material (Figs. 9–12) from where the latter subsequently spreads in circular or triangular manner until the primary wall is wholly or partially covered. Where secondary thickening remains localised to only a part of the wall such cells appear to remain physiologically active. Secondly, a simultaneous and progressive deposition of secondary wall material leads to a thickening of the wall of the whole cell (Figs. 13–17).



FIGS. 13–17.

Macerated pseudothalli. Fig. 13. Scalariform to reticulate secondary wall thickening in tracheary cell situated between two parenchyma cells of pseudothallus, safranin, $\times 400$. Fig. 14. Differentiating tracheary element in which secondary wall is laid down simultaneously in all parts of cell. Pit fields in primary wall are not covered, toluidine blue, $\times 400$. Fig. 15. Air-filled tracheary cell from terminal position on pseudothallus with vessel-like endplate (arrow). Thickening varies from scalariform to reticulate to pitted, safranin, $\times 400$. Figs. 16–17. Isolated tracheary cells. $\times 120$ and $\times 140$, respectively. Note vessel-like endplates (arrows), toluidine blue.

pf, pit field; st-rt-pt, scalariform to reticulate to pitted thickening; sw, secondary wall

Extraordinarily, in some cells secondary wall thickening clearly appears to occur on the outer surface of the cell wall (Fig. 12, 15). A definitive ultrastructural study would be necessary to elucidate the sequence of events involved here.

As regards type, there appears to be an intergradation of thickening from scalariform to reticulate to pitted, with the majority of elements probably best described as reticulate-pitted.

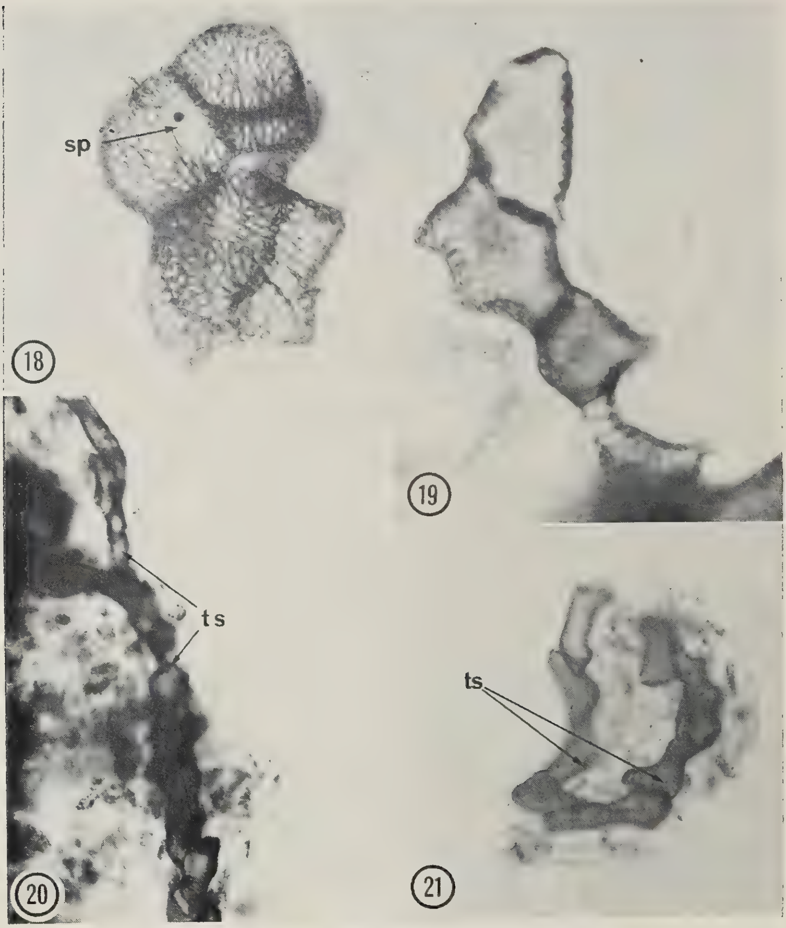
Function. It must be borne in mind that secondary wall formation in the differentiating tracheary elements of the pseudothallus is not influenced by surrounding cells; usually there are no adjoining cells. In partially differentiated tracheary cells functional chloroplasts are present (Fig. 11) but fully differentiated elements are devoid of contents. Parenchyma cells situated above fully differentiated tracheary elements eventually senesce and die or else differentiate, fully or partially, into tracheid-like cells. Consequently, it is unlikely that the function of these tracheary elements is one of conduction or storage; it probably is simply mechanical. Therefore, whether to refer to these tracheary elements as tracheids or vessels becomes a tenuous question.

Vessel-like members with what appear to resemble simple perforation plates (Fig. 16, 17) are found occasionally, as are tracheary cells with large, simple perforations scattered over the wall surface (Fig. 18). The usual ontogenetic progression of secondary wall thickenings apparent in the tracheary cells of primary xylem (Esau, 1960), is not a feature of the pseudothallial tracheary elements.

Aggregations of tracheary elements. Aggregations of tracheary elements in the compact, newly-proliferated tissue of the explant, appear to develop in one of three ways. Pseudothalli tend to intergrow and, particularly at the explant surface, become surrounded by parenchyma. Firstly, a localised differentiation of a few cells into tracheary elements occurs (Fig. 18). Surrounding such an islet of xylary cells and probably limiting its access to the external environment is a cambium-like sheath. Further development results in the formation of vessels and there is at least some evidence that roots arise from the peripheral cells of these vascular islets or nodules. Secondly, secondary wall thickening and lignification may occur in adjoining cells in one plane, probably along a hormonal and/or nutrient gradient, resulting in columnar files of tracheary elements (Fig. 19, 20). Thirdly, tracheary elements form in circular groups enclosing parenchyma in the centre (Fig. 21).

Conclusion

It is difficult to follow the development of the vascular tissues from serial sections because of the haphazard courses adopted by the xylary formations described above. Tracheary element and vascular nodule formation definitely



FIGS. 18–21.

Macerated tissue from dense, intergrown pseudothallial mass. Fig. 18. Islet of tracheary elements from within cambium-like zone. Note simple perforations which probably serve as vessel endplates, safranin, $\times 400$. Figs. 19–20. Columnar vascular strands, toluidine blue, $\times 400$ and $\times 150$, respectively. Fig. 21. Circular strand of tracheary elements enclosing parenchyma, toluidine blue, $\times 150$.

sp, simple perforation; ts, tracheid strand

are stimulated by high levels of auxin, and it seems clear that isolated pseudothallial tracheary cells, with subsequent parenchymatous proliferation, ultimately give rise to aggregations of vascular tissue from the surrounding cambial-like

cells of which roots have their origin. The function, as well as the factors which control differentiation of tracheary cells in a pseudothallus, remains obscure.

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ON THE OCCURRENCE OF *OPHIDOCLADUS* (RHODOMELACEAE) IN SOUTHERN AFRICA

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Abstract

Collections of *Ophidocladus* (Rhodomelaceae) from Moçambique and South Africa were studied and the relationship of this material with the type species (*O. simpliciusculus* (Crouan) Falkbg.) and other related taxa, is discussed in detail. Based on the vegetative and reproductive uniformity, it is concluded that the material of *Ophidocladus* from Europe, Southern Africa, Western Australia, North and South America is best included in the type and only species. Hence *O. californica* (Hollenberg) Kylin and *O. herposiphonioides* Joly et Yamaguishi are reduced to synonomy. A map showing the known distribution of *Ophidocladus* is given.

Uittreksel

DIE VERSPREIDING VAN *OPHIDOCLADUS* (RODOMELACEAE) IN SUIDLIKE AFRIKA.

Versamelings van *Ophidocladus* (Rhodomelaceae) uit Mosambiek en Suid-Afrika is bestudeer en die verwantskap tussen hierdie monsters en die tipe spesies (*O. simpliciusculus* (Crouan) Falkenberg), asook ander verwante taksa, is volledig bespreek. Op grond van die eenvormigheid van die vegetatiewe en voortplantingsstrukture, word dit afgelei dat die plante van *Ophidocladus* uit Europa, suiderlike Afrika, Wes-Australië, Noord- en Suid-Amerika by die tipe en enigste spesies hoort. Dus word *O. californica* (Hollenberg) Kylin en *O. herposiphonioides* Joly et Yamaguishi 'n sinoniem onder *O. simpliciusculus* verlaag. 'n Kaart word voorsien waarop die verspreiding van *Ophidocladus* aangegee word.

Introduction

While describing another rhodomelaceous alga, Pocock (1953: 43) mentions the occurrence of an undetermined species of *Ophidocladus* at Muizenberg, Cape Province, South Africa and an identical alga was subsequently recorded from Inhaca Island, Moçambique (Pocock, 1958). Since the nearest records of *Ophidocladus* are from the Canary Islands (Børgesen, 1930) and Western Australia (Falkenberg, 1901), a study of the southern African material was made in order to determine its relationship to the type species *Ophidocladus simpliciusculus* (Crouan) Falkenberg. In addition to the type species, the southern African material was also compared with the related *Ophidocladus californica* (Hollenberg) Kylin from the Californian coast, *Ophidocladus herposiphonioides* Joly et Yamaguishi from Brazil and *Polysiphonia obscura* Harvey from Western Australia. Other collections of *Ophidocladus* from southern African localities were also examined and the findings are given.

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MATERIAL EXAMINED

Type specimen—*Ophidocladus simpliciusculus* (Crouan) Falkenberg. Ex Herb. Crouan, Algues marines du Finistère, No. 302. (Now in PM—unnumbered.)

South Africa —Strandfontein, 19.ix.40 (Pocock, 3299)*.
Kasouga, 11.vi.44 (Pocock, 8165).
Cannon Rocks, Richmond, 23.x.44 (Pocock, 8223).
Muizenberg, 7.xii.45 (Pocock, 8568); 14.xii.51 (Pocock, 10200).
Sedgefield, 20.viii.51 (Pocock, 9317).
St. James, 19.xii.51 (Pocock, 10261).
Swartklip, 1.i.52 (Pocock, 10259).
Platboom, 14.i.52 (Pocock, 10294).
Kowie, Salt Vlei, 21.iv.60 (Pocock, 13965).
Kowie, Shark Bay, 21.iv.60 (Pocock, 13960).

Moçambique —Inhaca Island, 26.ix.57 (Pocock, 12162); 30.i.71 (Saenger, 594).

United States —Corona del Mar, California, 24.x.42 (Hollenberg, 3286).

Australia —King George's Sound (Harvey, TCD 182-B) (Annotated in Harvey's handwriting: "*P. simpliciuscula* Cr. fida. J. Ag. *P. obscura* Harv. (nec. Ag.)".
—King George's Sound (Harvey, TCD—unnumbered: annotated 'KGS' in Harvey's handwriting in addition to 'cf *Polysiphonia obscura*').

Unfortunately no herbarium specimens of *O. herposiphonioides* from Brazil were available and all comments and measurements are based on the descriptions and illustrations in Joly (1965) and Joly *et al.* (1963).

GENERIC LIMITS OF *Ophidocladus* FALKENBERG (1897)

The genus *Ophidocladus* was described by Falkenberg (1897) from a Crouan specimen of *Polysiphonia simpliciuscula*. According to Falkenberg, *Ophidocladus* is characterised by its peculiar thallus structure, consisting of an erect and prostrate system. The prostrate system is attached to the substratum by unicellular rhizoids and possesses 10—20 pericentral cells. It is dorsiventrally organized with the first pericentral cell cut off in a single dorsal row. No cortex is formed and trichoblasts are absent. This prostrate system gives rise to a number of dorsally inserted, endogenous erect branches, which, although lacking a cortex, do form trichoblasts alternating in two diametrically opposed rows. In contrast with the dorsiventral system, the erect branches are radially organised with a 1/2 divergence between successive trichoblasts.

* (All MAP specimens now housed in Albany Museum Herbarium (GRA)).

With the exception of the trichoblasts and the unicellular rhizoids, all branching is endogenous. In general, two tetrasporangia are produced in each fertile segment.

Another species (?*Ophidocladus schousboei* (Thuret) Falkenberg) provisionally placed in *Ophidocladus* by Falkenberg (1901) has subsequently been removed and placed in a separate genus *Leptosiphonia* as *L. schousboei* (Thuret) Kylin (1956: 509). The latter genus is readily distinguished from *Ophidocladus* by the exogenous branching of the fronds and the absence of a dorsiventral prostrate system.

Description of the Southern African Plants

A. Gross morphology

The fronds vary in height from a few millimetres to approximately 4 cm and generally form dense, extensive mats on sand-swept rocks in the lower littoral zone.

The prostrate system is attached to the substratum by a number of unicellular rhizoids issuing from the ventrally situated pericentral cells. The apices of the prostrate branches are curved towards the substratum (Figure 1) and produce 15—25 pericentral cells.

On the dorsal side of the prostrate system, erect branches arise endogenously at more or less regular intervals (3—6 segments, Figure 1). At first, these are curved towards the tip of the prostrate branches but they later become straight.

Fig. 1.
Apex of prostrate branch showing ventrally curved tip and the initiation of ventral rhizoids and dorsal endogenous erect branches.

In both prostrate and erect branches, there are 15—25 pericentral cells and no cortex is formed. At the apices of the erect branches, distichously inserted trichoblasts are produced.

Between successive erect branches, the prostrate branches produce paired lateral branches from one of the segments, eventually developing into new prostrate systems. Often only one of the pair develops into an indeterminate prostrate branch while the other remains only a few segments in length.

B. Apical segmentation

Segmentation of the prostrate branches occurs from a dome-shaped apical cell. The first pericentral cell of each segment is cut off dorsally and directly above that of the previous segment. The remaining pericentral cells then form

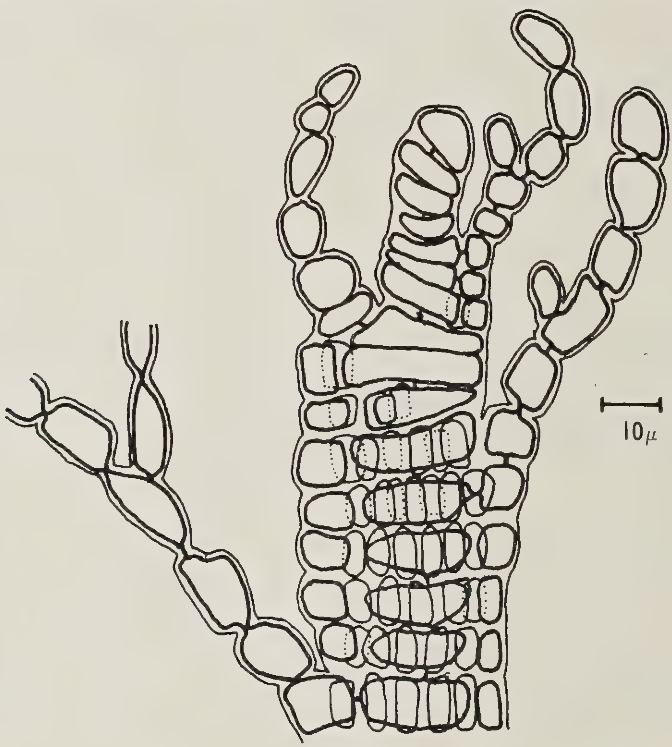

Fig. 2.
Apex of erect branch bearing alternate-distichously inserted trichoblasts. Note the formation of the first pericentral cell immediately below each trichoblast.

in an alternating sequence as generally found in the Rhodomelaceae. The endogenous erect branches emerge immediately in front of the first pericentral cell of that segment of the prostrate branch and consequently the erect branches are also produced in a single dorsal row (Figure 1).

Development of the erect branches proceeds by means of a dome-shaped apical cell forming discoid segmental cells. Every third or fourth segmental division is oblique and gives rise to a trichoblast initial (Figure 2). The trichoblasts are dichotomously branched, colourless and deciduous. The first pericentral cell of the erect branch is cut off immediately below the point of insertion of the trichoblast (Figure 2) and the remaining pericentral cells are then formed first to the left when viewed from above and then to the right and so forth until 15—25 pericentral cells have been formed in each segment. As the arrangement of the trichoblasts on the erect branches is alternate-distichous, the erect branches are radially organized with a 1/2 divergence between successive trichoblasts.

C. Branching

With the exception of the trichoblasts and the unicellular rhizoids, all branching is endogenous. From the prostrate system, dorsal endogenous erect branches are regularly initiated every 3—6 segments and thus constitute ordinary ('normal') endogenous branches. As the paired lateral prostrate branches also occur regularly between two successive erect branches, these paired laterals must also be considered as ordinary, endogenous branches. However, in older parts of the prostrate system, some adventitious, endogenous laterals are also formed and, together with the degeneration of some of the paired laterals, are responsible for the irregular appearance of the older parts of the prostrate system.

In the erect branches, all polysiphonous laterals are endogenous and mostly ordinary in origin. These laterals develop either from the trichoblast-bearing segment or from the segmental cell immediately below that bearing (or formerly bearing) a trichoblast (Figure 3). The first cell of the polysiphonous lateral emerges between the pericentral cells on that side where the trichoblast is (was) situated (Figure 3), resulting in the polysiphonous lateral being borne on the same side of the axis as the first pericentral cell of that segment (cf. Hommersand, 1963: 341). Hence, these laterals exhibit the same alternate-distichous arrangement as the trichoblasts. This type of branching represents ordinary endogeny (sensu Falkenberg, 1901; Saenger, 1970) since the polysiphonous laterals are directly related in their position to the ordinary, exogenous trichoblasts. Later in development, some adventitious endogenous branching of the erect branches also occurs, resulting in irregular branching of the mature fronds.

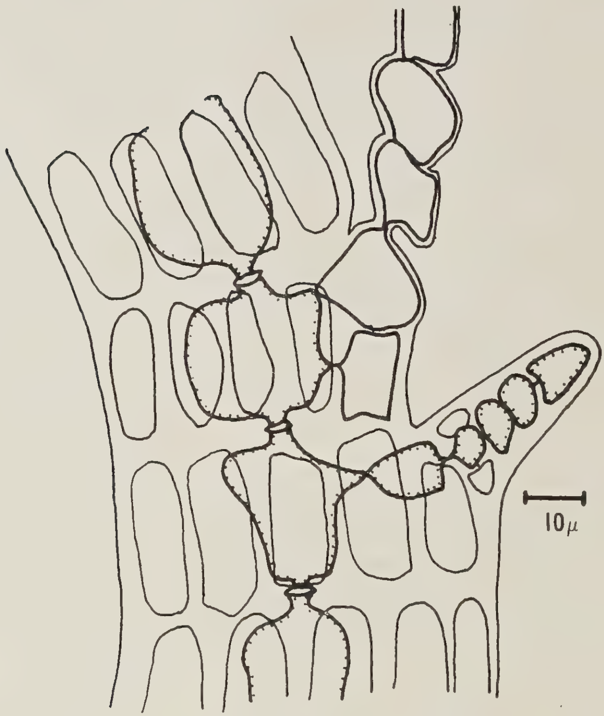

FIG. 3.
Production of an endogenous lateral from a segment immediately below that bearing a trichoblast.

D. Development of the procarp and cystocarp

Mature cystocarps generally develop only on cystocarpic plants but in several plants examined, such cystocarps were found on the tetrasporic plant (Figure 4).

The procarp always develops on a trichoblast and here, generally on the third segment (Figure 5). The basal segment of the procarpial trichoblast does not produce pericentral cells but the two following segments produce approximately 5—7 pericentral cells. One of the pericentral cells of the third segment acts as the supporting cell for the procarp and gives rise to one basal and 2 lateral sterile cells (Figure 5). A four-celled carpogonial branch is then formed from

Fig. 4.
Part of a tetrasporic plant bearing two lateral cystocarps on one of the lateral branches.

the supporting cell. The trichoblastic origin of the procarp can be seen by the continued monosiphonous growth of the trichoblast beyond the procarp (Figure 5).

Before fertilization, the pericarp is initiated by the repeated longitudinal divisions of the pericentral cells of the fertile segment and those immediately below it. No detailed observations were made on the processes of fertilization and gonimoblast formation. The mature cystocarp is globose to ovoid and more or less sessile (Figure 6). Remains of the sterile cells and a large fusion cell are present, the latter producing gonimoblast filaments bearing terminal carposporangia.

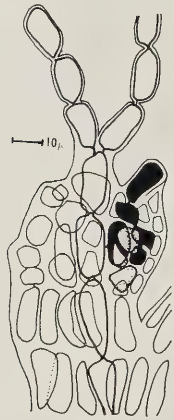

FIG. 5.

Trichoblast with fully developed procarp. Supporting cell and the carpogonial branch cells are black while the two lateral and one basal sterile cells are stippled.

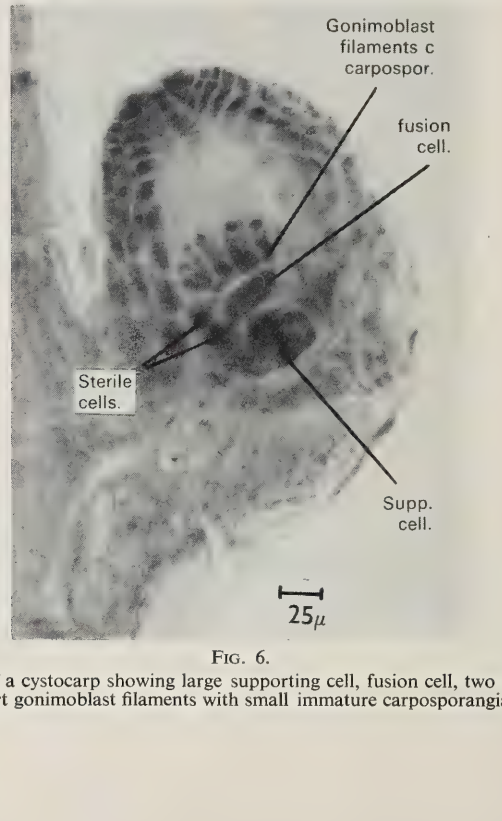

FIG. 6.

Optical section of a cystocarp showing large supporting cell, fusion cell, two sterile cells and short gonimoblast filaments with small immature carposporangia.

E. Development of spermatangia

Spermatangia are developed on the trichoblasts of the erect branches. These trichoblasts arise in an alternate-distichous manner (Figure 7a—e) at intervals of 2—5 segments. Like the sterile trichoblasts, the spermatangial trichoblasts are branched. While the basal segments form pericentral cells, the tips of the trichoblasts remain monosiphonous and free. Spermatangial mother cells are formed on the pericentral cells, each pericentral cell giving rise to 1—4 spermatangial mother cells. Between 2—8 spermatangia are then formed on each of the spermatangial mother cells. Overlapping of the spermatangial branchlets at the bases of the trichoblasts results in broad, cylindrical spermatangial branches measuring 60—300 μ in diameter (Figure 7e).

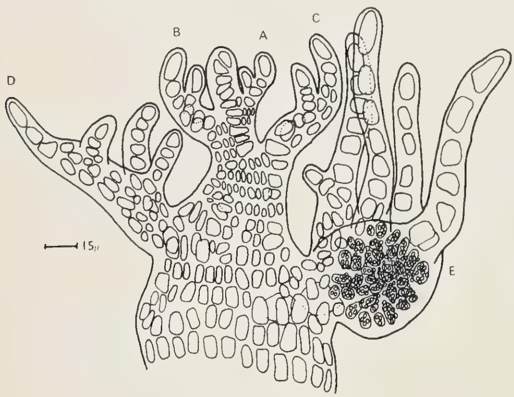

FIG. 7a—e.
Branch apex of male plant with developing spermatangial trichoblasts.

F. Development of tetrasporangia

Two tetrasporangia are usually produced per segment and are arranged in straight series in the terminal portions of the erect branches (Figure 4). The two sporangia lie in a plane perpendicular to the plane of insertion of the trichoblasts (cf. Hollenberg, 1943 fig. 11). Each fertile segment produces between 10—20 pericentral cells. The two fertile pericentral cells elongate radially and cut off two cover cells at their distal ends. The cover cells assume a size and shape identical to the sterile pericentral cells. No further division of the cover cells was observed. After cover cell formation, the sporangium is cut off in a median position on the pericentral cell. The tetrahedrally divided sporangium is 45—65 μ in diameter and is released through vertical slits between the sterile pericentral cells. It has not been possible to determine exactly which pericentral

cells produce the tetrasporangia but since the first formed pericentral cells lie in a plane at right angles to the tetrasporangia, it is likely that the sporangia are formed from the seventh and eighth pericentral cells.

Discussion

From the description given of the southern African plant, it can be seen that it readily agrees with the generic features of *Ophidocladus*. In 1943, Hollenberg described *Rhodosiphonia californica* from the Californian coast and separated this alga from *Ophidocladus* because of the manner of origin of the lateral branching. Hollenberg (1943) maintains that while *Ophidocladus* has ordinary, endogenous branching, *Rhodosiphonia* is characterized by adventitious, endogenous branching. Examination of the branching of *R. californica* showed it to be the same as in *O. simpliciusculus* from France and the African and Australian material. For reasons discussed earlier, this branching is considered ordinary although inconsistent development and later adventitious branching gives the appearance of an irregularly branched frond.

Falkenberg (1901) recognized that the lateral branches of the erect system of *O. simpliciusculus* were directly related to the position of the trichoblasts but he was inconsistent in his terminology. On p. 490, he states that "diese *Adventivsprosse** . . . nur von den blattbildenen Segmenten erzeugt werden und durch die Narbe des abgefallenen Blattes nach aussen treten." Yet on p. 55 of his work, Falkenberg states that as "die Stellung der . . . Sprosse gesetzmaessig geregelt ist, so muss man sie als *normale** Sprosse bezeichnen".

In addition to the ordinary laterals, truly adventitious laterals are formed later during development. It seems likely that the presence of both types of laterals led Hollenberg (1943) to conclude that the Californian alga differed from *Ophidocladus* in the manner of origin of the lateral branches.

Kylin (1956: 542) included the Californian plant in *Ophidocladus*, retaining it as a separate but closely related species because of its smaller size and sparser branching than in the type species.

Recently Joly *et al.* (1963) described *O. herposiphonioides* Joly et Yamaguishi from São Paula, Brazil. The habit of this plant with its prostrate and erect systems and the internal organization undoubtably confirm its inclusion in the genus *Ophidocladus* as previously defined. However from the descriptions and illustrations of this plant in Joly (1965) and Joly *et al.* (1963), there appears to be no valid reason for maintaining this alga as a species separate from *O. simpliciusculus* since the type and manner of branching and the formation of reproductive structures is identical to that found in *O. simpliciusculus* from other localities.

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* The italics are mine.

Comparisons of dimensions of certain features of the type specimen of *O. simpliciusculus* and specimens from California, Brazil, Moçambique, two South African localties and Western Australia (Table 1) shows the similarity of all the material. The internal organization of all the plants is identical and the dimensional variation between the specimens is no greater than that found in material from any one localtiy. In addition, the characteristic transverse banding of the cytoplasm of *O. californica* (Hollenberg, 1943) is also present in the southern African material and a re-examination of the type and Western Australian specimens, showed it in these plants as well. On occasions, three tetrasporangia are formed in the fertile segments of *O. californica* (Hollenberg, 1943) and similar occurrences were noted in the South African material.

TABLE 1
Comparison of dimensional data of *Ophidocladus* from a number of localities with the type specimen.

Character	*Ophidocladus simpliciusculus* TYPE	*Ophidocladus*					
		California	Muizenberg	Salt Vlei	Moçambique	Western Australia	Brazil*
Frond height (cm)	1—3	1—3	2—4	1—2	2—3	2—4	3—6
Branch diam. (μ)	100—150	80—140	90—200	90—150	100—160	100—150	100—180
Number of pericentral cells	12—20	14—20	15—25	15—18	16—18	12—22	17—27
Length/diameter of segments	0,7—1,0	0,7—1,0	0,6—1,3	0,5—1,3	0,6—1,0	0,7—1,1	0,8—1,6
Diameter of tetraspores (μ)	—	40—60	45—65	40—65	45—70	40—60	40—60
Diameter cystocarps (μ)	—	250—300	350—400	—	—	—	—
Diameter of spermatangial branches (μ)	—	90—300	60—300	—	—	—	150

* Data from Joly (1965) and Joly *et al.* (1963).

The separation of the Californian plant from the type species appears to be based on an incomplete analysis of the branching type and on trivial vegetative features such as size and density of branching. For some time the Australian specimens of *Ophidocladus* were considered as belonging to a separate species because of their geographical isolation (Falkenberg, 1901; Kylin, 1956). Other authors (Harvey, 1863; xxii; Børgesen, 1930; Lucas and Perrin, 1943; May, 1965) have included the Australian alga with *O. simpliciusculus* and comparisons with the other plants (Table 1) supports such an inclusion.

As the southern African material covers the whole range of vegetative variation and, as the reproductive structures are identical in all the material examined, it appears best to include all the plants presently placed in *Ophidocladus* in the type and only species.

NOMENCLATURE AND DISTRIBUTION

Based on the findings given above, the following synonomy applies:
Ophidocladus simpliciusculus (Crouan) Falkenberg 1897: 461.

Basionym—*Polysiphonia simpliciuscula* Crouan 1867: 157 (Dried specimens were distributed under this name in "Algues marines du Finistère, Fasc. I–III' No. 302, Brest, 1852).

Synonyms—*Polysiphonia obscura* Harvey 1854: 541 (non *Polysiphonia obscura* (Ag.) J. Agardh 1842: 123 = *Lophosiphonia obscura* (Ag.) Falkenberg 1901: 500).
Polysiphonia corallioides Suhr in Kuetzing 1864: 18.
Rhodosiphonia californica Hollenberg 1943: 573.
Ophidocladus californica (Hollenberg) Kylin 1956: 542.
Ophidocladus herposiphonioides Joly et Yamaguishi in Joly, Cordeiro and Yamaguishi 1963: 60.

The distribution of *Ophidocladus simpliciusculus* and its various synonyms is given (Figure 8). All distribution records are in latitudes between 25°—45° both in the northern and southern hemispheres. No records from within the tropics are available. It seems probable that further search will locate *O. simpliciusculus* in other areas of similar latitudes.

Since completion of this manuscript, herbarium material of *O. herposiphonioides* (SPF 2750, Praia do Pouso, Municipio de Parati, Est. Rio de Janeiro, Brazil, 10th May 1963), kindly made available by Dr. E. C. de Oliveira Filho of the Botany Department, Sao Paulo University, has been examined and has confirmed the suggestions regarding its conspecificity with *O. simpliciusculus*.

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FIG. 8.
Map of world distribution of *Ophidocladus simpliciusculus*. The type locality is ringed.

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GERMINATION INHIBITORS IN AQUEOUS SEED EXTRACTS OF FOUR SOUTH AFRICAN PROTEACEAE. *

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Abstract

The seed of many species of Proteaceae germinate very poorly. Four species belonging to this family viz., *Protea compacta*, *P. barbigera*, *Leucospermum cordifolium* and *Leucadendron daphnoides* were studied in an attempt to determine the underlying causes of poor germination. Seeds were germinated under three temperature regimes with or without treatment with fungicide.

Water extracts of seed coats and embryos of all species, when applied to test seeds of lettuce (var. Grand Rapids) and water cress, either inhibited seed germination or the growth of seedling roots, or both. A comparison of the effect of a range of sucrose solutions of known osmotic pressure, and the seed extracts (osmotic pressure determined cryoscopically) on lettuce seed germination showed that inhibition of germination by seed extracts could not be accounted for on the basis of osmotic pressure alone. Chromatographic separation of the water extracts of seed of all species in *iso*-propanol: ammonia:water (10:1:1 v/v) indicated a band of inhibition corresponding to Rf values of 0,9 and 1,0. Abscisic acid and coumarin separated in the same solvent system produced inhibition in the bio-assays which could not be distinguished from that produced by the seed extracts.

Uittreksel

ONTKIEMINGS-INHIBEERDERS IN WATEREKSTRAKTE VAN SAAD VAN VIER SUID-AFRIKAANSE PROTEACEAE.

Die sade van baie soorte van die Proteaceae ontkiem swak. Gevolglik is 'n studie gemaak van die ontkieming van vier soorte in die familie nl., *Protea compacta*, *Protea barbigera*, *Leucospermum cordifolium* en *Leucadendron daphnoides*, om te probeer vasstel wat die grondliggende oorsaak vir die swak ontkieming is. Die ontkieming van die saad is ondersoek by verskillende temperatuur-toestande in die aan- of afwesigheid van 'n swamdoder.

Die aanwending van waterekstrakte van saadhuide en embrios van al vier soorte, het óf die ontkieming, óf die wortelgroei van saailinge, óf beide, van slaai- (var. Grand Rapids) sowel as bronkhors-saad geïnhibeer. 'n Studie van die effek van 'n reeks sukrose-konsentrasies met bekende osmotiese druk en saadekstrakte (osmotiese druk krioskopies bepaal) op slaaisaadontkieming, het aan die lig gebring dat die inhibisie van ontkieming nie geheel-en-al aan die osmotiese druk van die saadekstrakte toegeskryf kan word nie. Chromatografiese skeidings van waterekstrakte van al vier spesies in *iso*-propanol: ammonia:water (10:1:1 v/v) het inhibisie getoon by Rf-waardes van 0,9 en 1,0. Absissiensuur en koumarien, geskei in dieselfde oplosmiddel, het inhibisie getoon in die biotoetse, wat nie van dié van die saadekstrakte onderskei kon word nie.

Introduction

One of the major obstacles to the large-scale cultivation of members of the South African Proteaceae is the fact that many are difficult to propagate.

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Although vegetative propagation by means of cuttings has proved successful and has certain advantages (Salinger, 1964; Rousseau, 1965, 1967; Topper, 1966) most plants are still raised from seed because the latter method requires relatively unspecialized facilities. The seed of many species, however, germinates very poorly, a fact long known to growers. Unfortunately, much of the literature on the propagation of members of the Proteaceae by seed is of a popular nature and is not very specific as to the treatments that have been used in attempts to improve germination (Thorns, 1943; Werner, 1951; Vogts, 1960).

Some preliminary laboratory work on seed germination in a number of species has been done (Atkinson, 1961; Horn, 1962; van Staden, 1966), but no clear-cut answers to the problem of poor germination have been obtained. Atkinson (1961) conducted investigations into seed germination in *Leucospermum catherinae*, but as very small samples of seeds were used, interpretation of her results is often very difficult. Horn (1962) maintained that poor germination in the Proteaceae was the result of ineffective seed screening methods. However, in his investigations and those of van Staden (1966) more effective seed screening methods were used and these still gave samples with a low percentage germination. Vogts (1960) suggested that the poor germination obtained in samples of proteaceous seeds was due to the presence of germination inhibitors within the seeds. She maintained that these inhibitors could be leached out, if the seeds were watered regularly. Horn (1962) did not regard germination inhibitors as being of importance in preventing germination of seed of this family.

Against the background of these conflicting experimental results and opinions, a series of investigations was initiated with the aim of determining the underlying causes of poor seed germination.

Materials and Methods

Plant material and germination techniques. An investigation was made of the germination of seed of *Protea compacta* R.Br., *Protea barbigera* Meisn., *Leucospermum cordifolium* (Salisb. ex Knight) Fourcade {= L. *nutans* R.Br.} and *Leucadendron daphnoides* Meisn. These particular species were chosen for study as they all have relatively large seeds which are more effectively sorted than the smaller sized seeds of many other species. Seed was carefully sorted and only apparently sound, undamaged seed was used in experiments. Seed used was purchased from the Department of Forestry, Pretoria and from M. J. Middelman, Newlands, Cape, South Africa.

At the outset of the investigation it was necessary to obtain some indication of the effect of temperature on the germination of seeds. Two hundred seeds of each species was germinated in growth cabinets under the three temperature regimes available to the authors. These were (i) alternating temperatures of 15°C

for 16 hours followed by 20°C for eight hours; (ii) alternating temperatures of 20°C for 16 hours, followed by 30°C for eight hours; and (iii) a constant temperature of 26°C. In (i) and (ii) light (ca. 1 lm/m^2) was supplied by cool white fluorescent tubes to coincide with the higher temperature period and in (iii) no light was supplied.

Seed was germinated in petri dishes on acid-washed sand. Distilled water was added to the sand until it was just moist and this level of moisture was maintained by the addition of further water when necessary. In order to test the effect of a fungicide treatment on germination, half the seeds of each species were soaked in 5% "Kaptan" solution for 30 minutes before being placed in the petri dishes. The criterion for germination was taken as the emergence of a healthy radicle approximately two mm in length. Germination counts were made daily for 63 days and seeds were removed from the petri dishes on germinating.

Leaching of Seeds. In order to determine whether a water-soluble inhibitor was present, 15 g of seed of each species was separated into two components viz., seed coats and embryos (which included cotyledons) and each component (unground) was shaken in 100 ml distilled water for 12 hours at room temperature. The leachate was filtered and the filtrate concentrated to 12 ml in a rotary flash evaporator at 40°C under reduced pressure. The inhibitor activity of the extracts was then tested in the lettuce seed and water cress seed bioassays.

Chromatography. Where extracts were separated this was done at room temperature using descending paper chromatography. The concentrated extracts were strip loaded on Whatmans No. 1 chromatography paper. The chromatograms were equilibrated for four hours prior to development. After the solvent front had travelled about 40 cm, the chromatograms were dried and cut into ten equal strips. The biological activity of each strip was determined in the lettuce seed bioassay. The extracts were separated in *iso*-propanol:ammonia: water (10:1:1 v/v).

Bioassays. At first it appeared that the ideal material for use in bioassays for the presence of germination promotors or inhibitors would be the excised embryos of the seed of each species. However, several attempts to grow these embryos on either filter paper or sand were not successful. Atkinson (1961) also failed in her attempts to germinate excised embryos of seed of *Leucospermum catherinae*. It was therefore decided to use the lettuce and cress seed bioassays.

(i) *Lettuce seed germination.* The influence of seed coat and embryo extracts on the germination of lettuce seed (Grand Rapids obtained from J. E. Ohlsen's Enke, Denmark) was investigated using the techniques of Sankhla and Sankhla (1968) and Wurzburger and Leshem (1969). Three millilitres of seed extract or distilled water (in the case of controls) were added to 50 lettuce seeds on two layers of Whatman No. 1 filter paper in a petri dish. Each treatment was repli-

cated four times. After the seed extracts or distilled water were added to the lettuce seeds, the latter were kept in the dark for two hours. The lettuce seeds were then exposed to cool white fluorescent light with an intensity of ca. $3{,}0 \times 10^2$ 1 m/m² for 30 mins. After illumination, the seeds were germinated in the dark in a growth cabinet maintained at 26°C. After 48 hours the percentage germination was recorded and the length of the root of each seedling was measured.

(ii) *Cress seed germination*. The cress seed germination test was also used to bioassay the seed extracts. The procedure followed was adapted from that of Valio and Schwabe (1970). Three millilitres of seed extract or distilled water (in the case of controls) were added to 25 cress seeds on two layers of Whatman No. 1 filter paper in a petri dish. Each treatment was replicated four times. Seeds were germinated in the dark in a growth cabinet at 26°C. Seeds were regarded as having germinated once the root tip had penetrated through the gelatinous layer surrounding the seed coat. After 48 hours the percentage germination was recorded and the length of the root of each seedling was measured.

Results and Discussion

Germination results after 63 days are shown in Table 1. In *Protea compacta*, *Leucospermum cordifolium* and *Leucadendron daphnoides* the germination percentage was significantly higher at 15°—20°C than at 20°—30°C. The same trend was shown by *Protea barbigera*, although differences were not statistically significant. Results for *P. cynaroides*, which were included for purposes of comparison, show indications of the opposite trend. However, differences were not statistically significant. It is interesting to note that the only seeds to ger-

Table 1

The effect of temperature on germination of seed of *Protea compacta*, *P. barbigera*, *P. cynaroides*, *Leucospermum cordifolium* and *Leucadendron daphnoides*.

Species	Temperature		Difference between temperatures
	15—20°	20—30°	
	Transformed means*	Transformed means*	
Protea compacta	28,45	18,04	10,41†
P. barbigera	32,07	26,22	5,85 N.S.
P. cynaroides	27,32	30,97	3,65 N.S.
Leucospermum cordifolium	25,94	4,93	21,0‡
Leucadendron daphnoides	34,32	15,42	18,90‡

* Angular transformation of percentages to degrees.
N.S. = Non significant.
† = Significant at 5% level.
‡ = Significant at 1% level.

minate at a constant temperature of 26°C were those of *P. cynaroides* (3%). The fungicide treatment brought about a reduction in germination in all species, but the effect was not statistically significant.

A relatively large proportion of the seeds failed to germinate. There are three possible reasons for this. Firstly, temperatures may not have been optimum for germination. Secondly, a large proportion of the seeds may have been infertile, possibly due to ineffective seed sorting. Thirdly, the seed may have been dormant due to the presence of an endogenous inhibitor. The first possibility cannot be ruled out completely because of the lack of data on optimum germination temperatures for the seed of South African Proteaceae. The second possibility appears to be unlikely as the seeds which failed to germinate by the end of the experiment were cut open and depending on species only 5—11 % of the seeds did not contain fully formed embryos. The most likely explanation for the poor germination appears to be that the seeds are dormant due to the presence of endogenous inhibitors or a lack of promotors, or both.

The presence of inhibitors was indicated in a study of the effect of the application of water extracts of seed coats and seed embryos on the germination and seedling root growth of Grand Rapids lettuce seed and cress seed (See Tables 2 and 3.)

Embryo extracts of *Protea compacta*, *P. barbigera* and *Leucospermum cordifolium* gave almost complete inhibition of germination when applied to test seeds of lettuce and cress. The application of the embryo extract of *Leucadendron daphnoides* gave germination results significantly (1 % level) below those of the distilled water controls.

TABLE 2

The effect of water extracts of seed of *Protea compacta* and *P. barbigera* on seed germination and seedling root growth of water cress and Grand Rapids lettuce.

Seed extract	Water cress		Grand Rapids lettuce	
	Seed germination	Seedling root growth	Seed germination	Seedling root growth
	Transformed means*	mean length (mm)	Transformed means*	mean length (mm)
Control (distilled water) .	59,88	13,20	80,20	11,22
P. compacta coat . . .	55,60	8,12	70,80	2,45
†*P. compacta* embryo . .	complete inhibition	complete inhibition	complete inhibition	complete inhibition
P. barbigera coat . . .	54,40	5,20	56,90	1,52
†*P. barbigera* embryo . .	complete inhibition	complete inhibition	complete inhibition	complete inhibition
Least significant P(0,05) .	9,69	0,73	6,57	0,84
differences P(0,01) .	14,68	1,11	9,97	1,27

* Angular transformation of percentages to degrees.

† Where germination was zero, treatments could not be included in a statistical analysis.

TABLE 3

The effect of water extracts of seed of *Leucospermum cordifolium* and *Leucadendron daphnoides* on seed germination and seedling root growth of water cress and Grand Rapids lettuce.

Seed extract	Water cress		Grand Rapids lettuce	
	Seed germination	Seedling root growth	Seed germination	Seedling root growth
	Transformed means*	mean length (mm)	Transformed means*	mean length (mm)
Control (distilled water) .	60,40	15,83	73,18	21,20
Leucospermum cordifolium coat	2,88	0,50	18,53	2,25
†*L. cordifolium* embryo .	2,88	0,25	Complete inhibition	Complete inhibition
Leucadendron daphnoides coat	33,93	2,43	58,55	3,85
L. daphnoides embryo . .	37,33	2,38	57,35	6,28
Least significant differences P(0,05) .	10,53	1,74	8,62	1,17
P(0,01) .	14,77	2,43	12,39	

* Angular transformation of percentages to degrees.

† Where germination was zero, treatments could not be included in a statistical analysis.

Water extracts of seed coats, in general, did not give such marked inhibition, but nevertheless germination results were still significantly below those of the distilled water controls. The seed coat extract of *Leucospermum cordifolium*, however, was the exception and gave particularly marked inhibition of germination in both bioassays. It is also apparent that the seed coat extract of *Protea compacta* brought about less inhibition of germination than the seed coat extracts of *P. barbigera* and *Leucadendron daphnoides*.

The fact that the seed coat and embryo extracts of all species had, to some extent, an inhibitory effect on lettuce and cress seed germination and seedling root growth suggested that in addition to the possibility of the presence of a chemical inhibitor, the osmotic pressure of the extracts might be exerting an inhibitory effect. In order to obtain some indication of the effect of osmotic pressure on the germination of lettuce seeds, samples were germinated on filter paper moistened with sucrose solutions ranging in molarity from 0,025 M to 0,4 M (corresponding to osmotic pressures ranging from 0,66 bars to 11,2 bars) (See Figure 1). This figure shows a curve very similar to that obtained by Lerner, Mayer, and Evenari (1959). These workers germinated lettuce seed on a range of NaCl solutions giving osmotic pressure values from 0,5 to 8,1 bars. Whereas they obtained complete inhibition of germination at O.P = 6,1 bars, in the present study complete inhibition of germination occurred at O.P. = 8,1 bars.

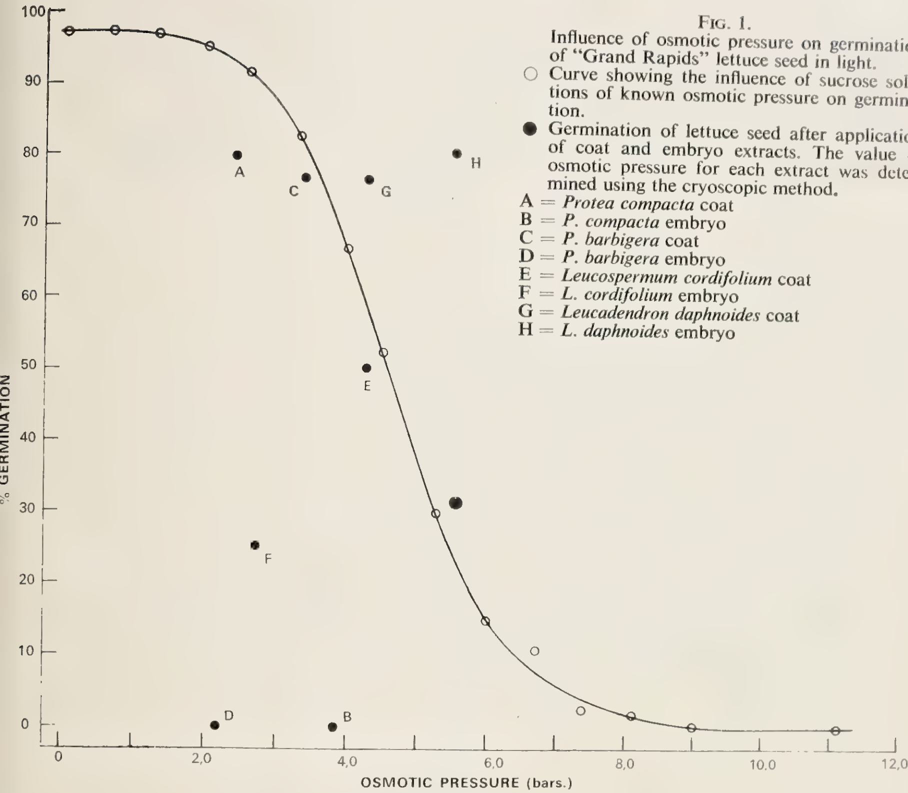
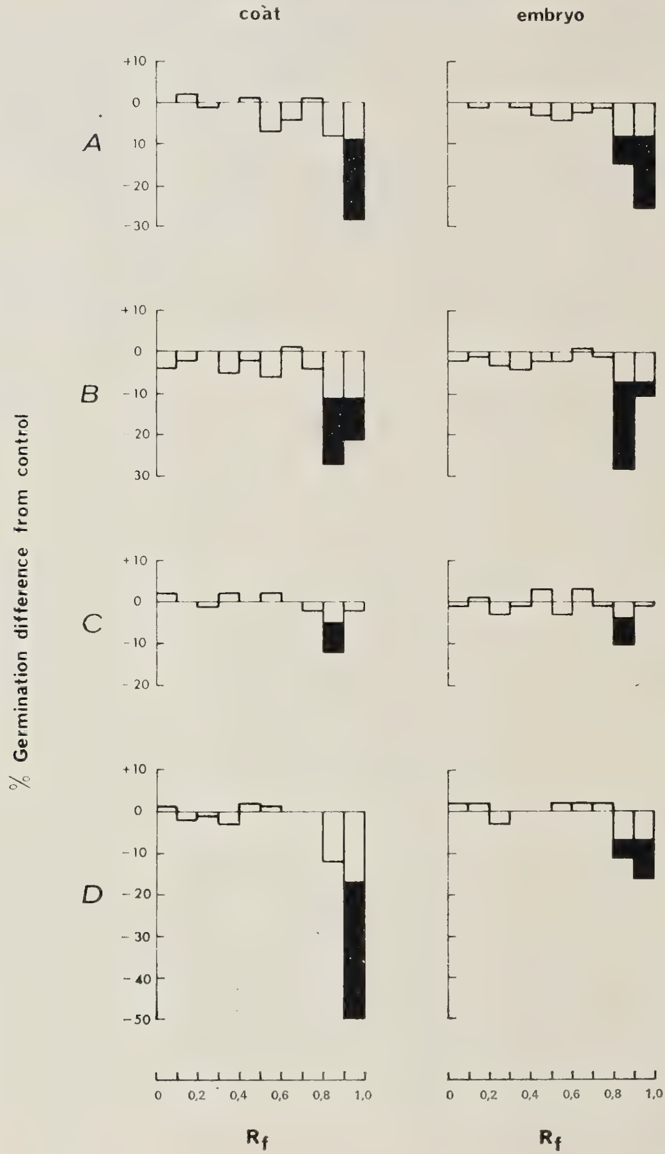


FIG. 1.
Influence of osmotic pressure on germination of "Grand Rapids" lettuce seed in light.
○ Curve showing the influence of sucrose solutions of known osmotic pressure on germination.
● Germination of lettuce seed after application of coat and embryo extracts. The value of osmotic pressure for each extract was determined using the cryoscopic method.
A = *Protea compacta* coat
B = *P. compacta* embryo
C = *P. barbigera* coat
D = *P. barbigera* embryo
E = *Leucospermum cordifolium* coat
F = *L. cordifolium* embryo
G = *Leucadendron daphnoides* coat
H = *L. daphnoides* embryo

The osmotic pressure of each seed extract was determined using the cryoscopic method. These seed extracts were then applied to lettuce seed which was treated as in the bioassay. Seed extract osmotic pressure values and the corresponding lettuce seed germination results were then plotted on Figure 1.

Six of the eight seed extracts gave germination results below those obtained with sucrose solutions of equivalent osmotic pressure. The remaining two, viz the seed coat and seed embryo extracts of *Leucadendron daphnoides*, gave germination results slightly above those of the sucrose solution of equivalent osmotic pressure. Table 3, shows that these latter two extracts, although not influencing germination, to the same extent as the other seed extracts did reduce seedling root growth significantly (1 %).


coat
embryo
A
B
C
D
% Germination difference from control
+10
0
10
-20
-30
-10
20
30
-40
-50
0
0,2
0,4
0,6
0,8
1,0
Rf

All the extracts have values of osmotic pressure which fall within the range of 0,56—6,1 bars, which Lerner and Evenari (1961) designate "the region of combined osmotic pressure and chemical inhibition".

This tends to indicate that the results in Tables 2—3 and Figure 1 cannot be explained on the basis of osmotic pressure alone and that there appears to be one or more chemical substance present in the seed extracts, which either inhibits germination or seedling root growth or both.

Further evidence of the presence of an inhibitor was shown in the bioassay of the chromatographed seed extracts. Figure 2 shows the lettuce seed bioassay results after the separation of the extracts in *iso*-propanol:ammonia:water. The seed coat and seed embryo extracts of all species showed a band of inhibition corresponding to Rf values 0,9—1,0. These results were compared with the inhibitory effects of two widely occurring germination inhibotors viz. coumarin and abscisic acid (ABA) which were separated in the same solvent system (Fig. 3). The coumarin standard alone gave a band of inhibition corresponding to Rf values 0,9—1,0 and the ABA standard alone gave inhibition at Rf 0,8—0,9. A mixture of the two standards gave inhibition at Rf 0,8—0,9. Thus in this solvent system the inhibitory effects of the two standards could not be distinguished and the band of inhibition shown by the seed extracts corresponded with both ABA and coumarin.

Germination inhibitors have thus been shown to be present in the seed extracts and the possibility exists that they may play a role in the regulation of seed germination under natural conditions. There are also some indications that the inhibitors present in the seed extracts have properties similar to either ABA or coumarin or both. Further work remains to be done to characterize the inhibitor(s) more clearly.

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The authors are grateful to Professor F. T. Addicott of the University of California, Davis for reading the manuscript and for his helpful criticism. Thanks are also due to Mr. Veda Sarawan for technical assistance.

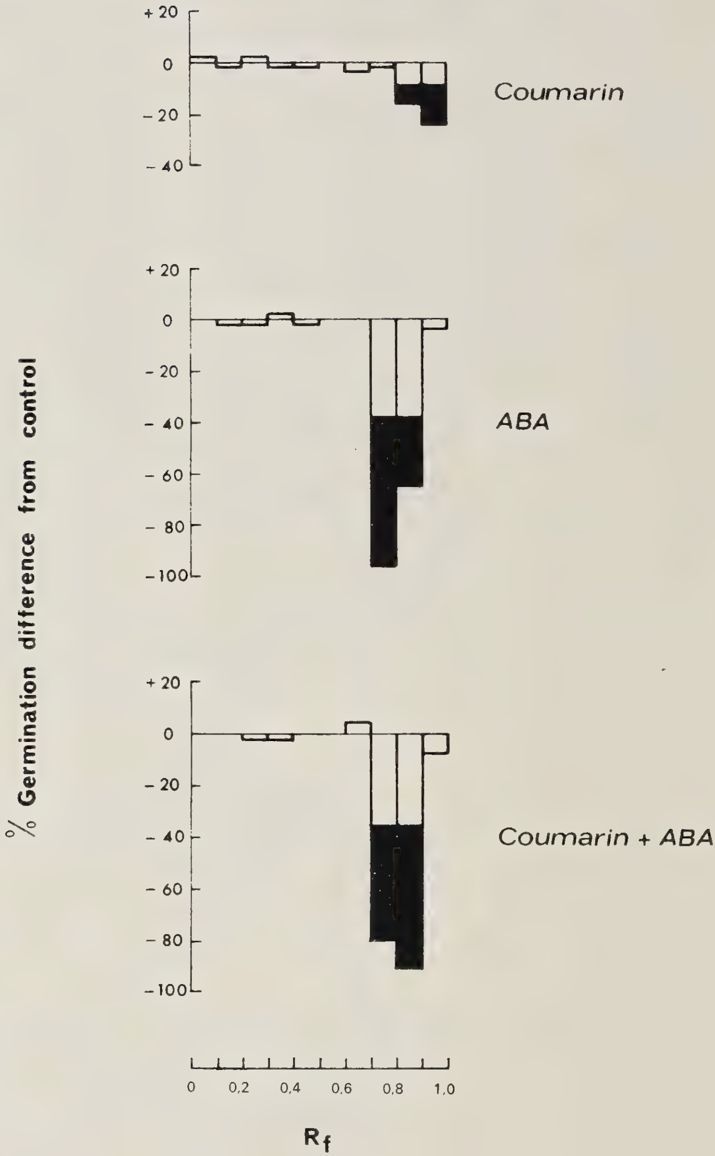
Fig. 2.

A comparison of the effects of water extracts of seed coats and embryos on germination of "Grand Rapids" lettuce seed in light.

A = *Protea compacta* C = *Leucospermum cordifolium*

B = *P. barbigera* D = *Leucadendron daphnoides*

The solvent was *iso*-propanol:ammonia:water. Shaded areas represent differences significant at 1% level.



% Germination difference from control
+ 20
0
- 20
- 40
Coumarin
+ 20
0
- 20
- 40
- 60
- 80
- 100
ABA
+ 20
0
- 20
- 40
- 60
- 80
- 100
Coumarin + ABA
0
0,2
0,4
0,6
0,8
1,0
R_f

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Fig. 3.

A comparison of the effects of ABA and coumarin on the germination of "Grand Rapids" lettuce seed in light. The solvent was *iso*-propanol:ammonia:water. The shaded areas represent differences significant at the 1% level.

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CYTOLOGICAL AND MORPHOLOGICAL STUDIES IN THE SOUTHERN AFRICAN IRIDACEAE

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Abstract

This work is a cytological and morphological study of the southern African representatives of the Iridaceae. Hybridisation in the family is surveyed and several intergeneric crosses were attempted. A detailed examination of the chromosome cytology of several species in each genus was made. In all, 225 species in 43 genera were studied, 186 of these being new chromosome records, including 23 new reports for genera. The results were correlated with morphology and where applicable, with anatomy, and compared critically with the existing systematic treatments of the family. A new classification into tribes and subtribes is presented, and the circumscription of several genera is altered. As a result several changes in nomenclature were made, including a number of new combinations. The genus *Anomatheca* is upheld (previously a subgenus of *Lapeirousia*) while *Curtonus*, *Anaclanthe*, *Petamenes* and *Kentrosiphon* are reduced to synonymy. It is also suggested that *Acidanthera* be incorporated in *Gladiolus* but the necessary nomenclatural changes were not made.

Uittreksel

SITOLOGIE EN MORFOLOGIESE STUDIES IN DIE SUID-AFRIKAANSE IRIDACEAE.

Hierdie werk is 'n sitologiese en morfologiese studie van die Suid-Afrikaanse verteenwoordigers van die Iridaceae. Verbastering in die familie word ondersoek en 'n poging is aangewend om verskeie intergenetiese kruisings te doen. 'n Gedetailleerde ondersoek van die chromosoom sitologie van verskeie spesies in elke genus was gedoen. Daar was 225 spesies in 43 genera bestudeer, 186 van hierdie is nuwe chromosoom rekords en 23 nuwe verslae vir genera. Die resultate was met die morfologie gekorreleer en waar toepaslik, ook met anatomie, hulle was ook krities vergelyk met die bestaande sistematiese behandeling van die familie. 'n Nuwe klassifikasie in die stamme en substamme word voorgestel en die omskrywing van 'n paar genera is verander. Dus word verskeie naam veranderings gemaak sowel as 'n paar nuwe kombinasies. Die genus *Anomatheca* bly onveranderd (voorheen 'n subgenus van *Lapeirousia*) terwyl *Curtonus*, *Anaclanthe*, *Petamenes* en *Kentrosiphon* weer sinonime word. Dit word ook voorgestel om *Acidanthera* by *Gladiolus* in te lyf maar die noodsaaklike naam veranderings is nie gedoen nie.

KEY TO THE CHAPTERS *Page*

This work represents part of a thesis presented for the Ph.D. degree in the Faculty of Science at the University of Cape Town.

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Introduction

The Iridaceae comprise a fairly large and homogeneous family of *Monocotyledonae.* It is agreed by most authors to be closely related to the *Liliaceae* and it is usually placed in the same order, *Liliales* although Hutchinson created a new order, *Iridales* for this family alone.

The distinguishing features of the family are its tricarpellary gynoecium with an inferior ovary, three stamens and equitant (isobilateral) leaves. There are exceptions to this last character in a few specialised genera, but here, the leaves are derived from the equitant type.

The classification of the family is in rather a confused state. Few authors agree as to the number or rank of the major groupings. Both the number of tribes (or sub-families) and the genera in them vary considerably and there is little agreement about which characters are significant in the classification of taxa above the specific level.

At present the family consists of about 65 genera and 1800 species. The size of the genera varies greatly as there are several monotypic groups, while others like *Iris* and *Gladiolus* contain more than 200 species. The distribution is worldwide but the region of greatest concentration is Africa, south of the equator. In southern Africa alone there are about 45 genera and 900 species recorded.

The figures quoted are necessarily rough estimates as few workers are agreed as to the number and limits of many genera and little general work has been done on the family for many years. Several genera urgently require revision and will probably be found to comprise fewer species than are at present recognised.

The present work is an attempt to elucidate some of the problems concerning classification and phylogeny and deals predominantly with South African taxa. The work involves a cytological investigation of the family, a new approach differing from the traditional use of only morphological characters for the classification of this group. It was hoped that certain morphological and cytological features could be linked so that the more significant characters for classification would be recognised. With the determination of these characters the rather vague and often arbitrary generic groups may then be recognised. In this way it is hoped that a better understanding of the family will be reached which may lead ultimately to the establishment of a natural classification.

Cytological studies of families and genera of plants have often proved extremely useful in solving problems of classification and taxonomy. The value of this aspect of investigation has been demonstrated amply by Levitsky in the Ranunculaceae, (fide Stebbins 1950), Babcock (1947) in *Crepis* and Simonet (1934) in *Iris*. In these studies confused or ambiguous situations, which could not be explained by extensive morphological investigation, were elucidated.

As cytotaxonomic studies deal mainly with chromosomal characteristics, it often happens that information on the phylogeny of generic groups is revealed and light is sometimes shed on methods of speciation, for example polyploidy and aneuploidy. The work of Raven and Kyhos (1965) on the evolution of the *Magnoliales* is an example of cytology indicating how evolution may have occurred. The use of chromosome studies in generic and specific taxonomy and in evolution is dealt with fully by Stebbins (1950), and in general his terminology and approach have been followed.

Little work has been done on the chromosome cytology of the Iridaceae. About one third of the genera have been examined, but quite randomly. Four genera only, *Crocus*, *Iris*, *Gladiolus* and *Romulea*, have been adequately investigated.

Owing to the numbers of species involved and the difficulty in obtaining live plants from other parts of the world, only the southern African genera are dealt with fully. As has been indicated, the majority of genera occur in this region and so it is hoped that a classification of these genera will prove significant for the classification of the family as a whole, or if not, at least show the line further investigation should take.

1. MATERIALS AND METHODS

A large number of species, representing as many genera as possible, was collected. Most often plants were collected in the field, though in some cases they were obtained from reliable horticultural sources. Wherever possible voucher specimens have been prepared, and unless otherwise stated, these were collected by the author and are housed at the Bolus Herbarium, Cape Town.

Lists of the species studied, together with the original localities and collector's number are given in tables in the chapters and sections dealing with the genera concerned (the abbreviations of herbaria are according to Index Herbariorum).

Chromosomes were studied mainly from mitosis in root tips and occasionally pollen mother cells were examined for meiotic phases. Although wild plants were almost invariably studied, it proved impractical to obtain root tips from plants in their natural state as the root system was usually found to be too extensive when they could be recognised in the field. The usual procedure was to collect plants in their native habitat and to let these dry off until the next growing season: spring in the summer rainfall area and autumn in the winter rainfall area. At this stage the corms were placed on damp sand in pots and the root tips harvested as they were produced. After sufficient root tips had been obtained, the corms were planted a few inches deep and grown to maturity when flowers could be obtained for further study if required. In the case of rhizomatous species, or when corms were not available, the root tips were obtained from germinating seeds or seedlings.

Root tips were harvested after midday on warm days as experience showed that this time was satisfactory, though not always optimum, for the observation of clear metaphase figures. The root tips were treated as follows:

Cytological Methods

Both wax section and squash methods were tried. In the former, root tips were fixed in Craf (Randolph 1935) and stored in 70% ethanol, or dehydrated immediately in a graded ethanol-n-butanol series, embedded in paraffin wax and sectioned 14—18 microns thick.

Two staining procedures were employed; either the aqueous Crystal Violet technique according to Smith (1934) or the Feulgen technique in which the method of preparation suggested by Kaston and Burton (1959) was used. Though initially the crystal violet stain gave good results, it was found to be unreliable and subsequently the Feulgen stain was used entirely.

When the squash method was used, root tips were pretreated in 0,05% colchicine for four hours and then fixed in acetic-ethanol, 1:3 for 10—15 minutes after which they were stored in 70% ethanol. After maceration in N-HCl at 60°C for about 8 minutes the meristematic portion of the root tips was placed in a drop of aceto-orcein (la Cour 1941) or lacto-propionic orcein (Dyer 1963) and squashed under a coverslip.

Preparations of pollen mother cells were obtained by squashing fresh anthers directly on to slides and staining in aceto-orcein or lacto-propionic orcein.

After experimenting with the various methods, it was decided that the paraffin wax section method would be followed. This was because although the squash method gave good results it was not suitable for species with small chromosomes as these could only be seen with difficulty. The wax section method also had the advantage of yielding permanent preparations which could be viewed at leisure and referred to subsequently. Permanent mounts with the squash method could only be obtained with difficulty and were frequently not satisfactory, although using the lacto-propionic orcein of Dyer, material did last for a few weeks. Squash preparations were, however, frequently made for plants with very large chromosomes as these could often be studied more easily than in sections, particularly if the chromosome number was high.

Drawing Technique and Representation of Karyotypes:

All cytological drawings were made with the aid of a camera lucida and a $25\times$ ocular. Although many metaphase plates were drawn for each species, only a single illustration is shown in this work. All the chromosomes illustrated were drawn from wax section preparations and are thus directly comparable.

Where chromosomes details were distinct, and homologous chromosomes could be recognised, the karyotype has been represented diagrammatically by means of an idiogram. This represents the haploid complement of chromosomes and greatly facilitates comparision of different karyotypes. The idiograms are compiled from at least three good metaphase plates and as there is always some variation in observed chromosome size owing to the degree of condensation, the idiogram may not exactly match the particular metaphase illustrated.

2. CLASSIFICATION SYSTEMS OF THE IRIDACEAE

The four important basic systems of classification of the Iridaceae are those proposed by Bentham & Hooker (1883), Pax (1888), Hutchinson (1934) and Lewis (1954). Earlier systems such as that of Klatt (1882) were based on too little information and are not of any importance today.

1. The classification of Bentham & Hooker.

In this very early classification of the family, it was divided into three tribes:

Moraeeae, *Sisyrinchieae* and *Ixieae*. The tribes were defined as follows:—

Moraeeae:	inflorescence a cymose corymb; flowers fugitive; stamens opposite the style branches.
Sisyrincheae:	inflorescence a cymose corymb; flowers fugitive; stamens alternate to style branches.
Ixieae:	inflorescence a spike; flowers not fugitive.

The only tribe which Bentham & Hooker subdivided was the *Sisyrinchieae* where they created four subtribes, defined as follows:

Croceae: rootstock a tunicate corm; spathes single flowered; scape single flowered.

Cipureae: rootstock a tunicate corm; spathes 2-flowered perianth tube short or absent; perianth segments subequal.

Eusisyrinchieae: rootstock a rhizome; spathes 2-flowered; perianth tube short or absent; perianth segments equal or subequal in most or inner segments smaller.

Aristeae: rootstock a short or creeping rhizome, or roots arising from a woody stem; perianth tube developed to some extent; capsule often included in the spathes.

The system was followed by Baker in Flora Capensis (1896) and also by Diels (1930) in the second edition of Engler & Prantl's *Pflanzenfamilien*, although he altered the sequence to place the *Moraeeae* at the end instead of the beginning. This system also formed the basis of Hutchinson's system.

2. The classification of Pax.

This classification, produced in 1888, appeared in the first edition of the *Pflanzenfamilien* of Engler & Prantl. Here the family is divided into three sub-families: the *Crocoideae* (Bentham & Hooker's subtribe of the *Sisyrinchieae*), the *Iridoideae* corresponding to the *Moraeeae* and the remainder of the *Sisyrinchieae*, and the *Ixioideae* corresponding to the *Ixieae* of Bentham & Hooker. These sub-families were defined as follows:

Crocoideae: reduced plants with solitary flowers lacking an aerial stem.

Iridoideae: inflorescence a many flowered cyme enclosed in spathes borne on an aerial stem.

Ixioideae: inflorescence a spike composed of many solitary flowers enclosed in spathes.

Here great stress is placed on the inflorescence. This is unsatisfactory as there are many different interpretations of the Iridaceous inflorescence and there are several exceptions at both specific and even generic levels in each sub-family. Pax subdivided his *Iridoideae* and *Ixioideae* into several tribes. In the *Iridoideae* he recognised four tribes, two out of Bentham & Hooker's *Moraeeae* and two out of their *Sisyrinchieae*. Pax changed the position of one group, the *Cipureae* as he removed it from amongst the *Sisyrinchieae* (of Bentham & Hooker) to a position in the tribe *Tigrideae* among genera which Bentham & Hooker regarded as belonging in their *Moraeeae*.

In Pax's system the *Ixieae* are for the first time divided into tribes. His basis for division was the nature of the flower and style branches. The tribes and their characteristics are as follows:—

Ixieae: flower actinomorphic; style branches undivided.
Gladioleae: flower zygomorphic; style branches undivided.
Watsonieae: flower zygomorphic; style branches divided.

This system was followed by Rendle (1904) and by Marloth (1915) in his Flora of South Africa. It has been superseded by that of Diels (1930) who reverted to the Bentham & Hooker system.

3. The classification of Hutchinson.

Hutchinson proposed a third classification of the Iridaceae in his *Families of Flowering Plants* (1934). He placed the Iridaceae alone in the order *Iridales* and within the family recognised eleven tribes of equal rank. The system is essentially that of Bentham & Hooker, though their tribes are divided and the genera arranged slightly differently. The *Moraeeae* are divided into three, the *Sisyrinchieae* into four (including the *Crocoideae* of Pax as one) the *Ixieae* into three, and one new one is created consisting of a primitive genus *Hewardia* or *Isophysis*, the presumed Iridaceous ancestor which has six stamens. In making his groups all of equal rank, the natural relationship between some of the tribes is obscured and this makes the system seem artificial and difficult to follow.

For his classification Hutchinson used quite different criteria from previous workers. The type of rootstock is considered important, especially for recognition of genera, but greatest significance is given to the flower and its progressive zygomorphy. This classification appears to be rather different from the previous two, but is actually similar except that the rank of several groups is changed.

The system of Bentham & Hooker and correspondingly of Hutchinson, was modified by Weimarck (1940). He considered that as the *Sisyrinchieae* are characterised by the lack of a perianth tube and the *Aristeae* by having one, *Aristea* itself was misplaced for it lacks a perianth tube. Thus he placed this genus in the *Sisyrinchieae* and the remaining genera of the *Aristeae* in the *Niveniinieae*, a new tribe, thus abolishing the tribe (or subtribe) *Aristeae*.

4. The classification of Lewis.

Lewis (1954) proposed a fourth classification of the family. She dealt only with South African species and recognised three tribes distinguished as follows:—

Irideae: inflorescence not spicate; flowers fugaceous, pedicellate and arranged in cymes.
Nivenieae: as above, but flowers not fugaceous; plants shrubby and exhibiting secondary growth.
Ixieae: inflorescence usually a spike; flowers not fugaceous, sessile with perianth tube.

This classification is most similar to that of Pax although the highest rank is the tribe, not subfamily. Lewis placed the woody genera in a tribe apart from *Aristea* with which they are usually grouped, for she considered their shrubby habit and secondary growth as very distinct features. Following Pax, the rather primitive *Aristea* is placed in the same tribe as *Moraea* and its allies, though in different subtribes. Lewis disregarded Pax' major group, the *Crocoideae* and she shows conclusively that it was an artificial unit comprising genera belonging to the *Irideae* and *Ixieae*.

3. HYBRIDISATION

Other than in the genera *Iris*, *Crocus* and *Gladiolus*, comparatively little critical work has been done on hybridisation in the Iridaceae. In other attractive cultivated genera many species have been hybridised to some extent by horticulturists.

There is a large number of hybrids in *Iris* and *Crocus*. Among these are some carefully produced experimental hybrids and here meiosis has been studied (Simonet 1934). Studies of hybrids in *Iris* have been of great value in suggesting the origin of some species (Randolph and Mitra 1959) and have also indicated the interrelationships and possible evolution of the different sections of *Iris* (Simonet 1934).

No comparable work has been done on any of the other genera except *Gladiolus*, where hundreds of crosses have been made in the search for new, horticulturally valuable forms. This work has been reviewed by Bamford (1935; 1941) and has recently been discussed by Hamilton (1968). It is known that several levels of polyploidy occur in *Gladiolus* and Bamford's work has shown that the diploid species are interfertile and produce fertile offspring. The diploid species can also be crossed with polyploids; the offspring in these crosses are not fully fertile but can be back crossed to some extent to the diploids. Most of the commercial varieties of *Gladiolus* are high polyploids and are the result of interbreeding between several different species. Intergeneric crosses among *Gladiolus* and *Homoglossum* or *Acidanthera* have also been reported and this will be discussed fully in the section on *Gladiolus* and its allies.

In other genera which are frequently grown in gardens most crossing appears to have been quite random and even accidental. In this manner numerous hybrids of *Tritonia*, *Sparaxis*, *Watsonia*, *Ixia*, *Babiana* and *Freesia* have come into existence and many of these have been named or even described as distinct species (Brown 1935; Goldblatt 1969). Because of its horticultural value, *Freesia* has received much attention from plant breeders. Attempts have been made to find wild species with which to increase variation in the cultivated forms; these are derived from only a few species according to Brown (1935). The varieties of *Freesia* cultivars are the product of considerable selection and

today almost all garden *Freesias* are polyploid. Many of the hybrids of *Ixia* now in cultivation are also polyploid (Brittingham, 1934) and it is likely that many forms in other cultivated genera are polyploid.

As hybrids are so easily obtained and many of the cultivated forms are polyploid, it is clear that cytological studies in the family must be done only on specimens collected in the wild. Those obtained from commercial sources will always be suspect and indeed are a likely source of many of the anomalous chromosome counts reported from time to time.

The studies in *Romulea* by de Vos (1965) have added to the information on hybrids in the Iridaceae. She reports that a few natural hybrids between closely related species occur. However, under artificial conditions many more hybrids can be obtained. Her results show that in general, related species with similar or the same chromosome numbers will hybridise and produce viable offspring, but in some cases the crossing of related species and varieties unexpectedly fails and it must be presumed that there is a reproductive barrier between these forms. The more distantly related species cross less easily, or not at all, which is not surprising in a genus where such a great range of chromosome numbers occur.

In a valuable study of hybridisation in *Watsonia*, *Ixia* and *Sparaxis*, Horn (1962) showed that most species in each genus are interfertile and yield fully fertile offspring. He found that species in these genera are normally cross-pollinated and that species were self-compatible, but when selfed, produced very few seeds. This observation can be confirmed by the present author for *Ixia* and *Sparaxis*. It is clear, however, that this phenomenon is not universal in the Iridaceae, for all *Gladiolus* species grown by the author are self-sterile and do not set seed unless cross-pollinated.

The ease with which Horn produced interspecific hybrids explains why so many garden hybrids occur. Hybrids are rare in nature although they have been reported in *Watsonia* and *Babiana* by Lewis (1950; 1959). Several putative hybrids exist in herbaria but these are by no means proven. The fact that natural hybrids are so uncommon suggests that external isolating factors operate to prevent interspecific hybridisation taking place.

As it is clear that there is little difficulty in obtaining interspecific hybrids and that these would in any case contribute little to the existing knowledge of interrelationships in the family, the author has in most cases attempted to produce intergeneric hybrids. It was presumed that any successful crosses would indicate close generic relationships or at least indicate certain affinities. Not surprisingly, few of these crosses proved successful but several interesting results were obtained. (Table 1).

Crosses were only attempted where some measure of success could be expected. Thus genera were crossed when it was known or suspected that these

were related or had a similar karyotype. Crosses were made in the normal way by emasculation before anthesis, bagging and transferring pollen to the isolated stigmas when these were receptive. Wherever possible reciprocal crosses were made.

The significance of the results of each cross will be discussed in the relevant section on each group of genera.

TABLE 1

List of interspecific and intergeneric crosses made by the author. The results of each cross and condition of any offspring are indicated.

Crossing	Normal Seed in Fruit	Hybrids
Dierama pendulum × Ixia conferta	0	—
Ixia conferta × Dierama pendulum	0	—
Hesperantha vaginata × Geissorhiza leipoldtii aff.	0	—
Geissorhiza leipoldtii aff. × Hesperantha vaginata	2	No germination
Moraea ramosissima × Dietes bicolor	0	—
Dietes bicolor × Moraea ramosissima	0	—
Dietes vegeta × D. bicolor	0	—
Dietes bicolor × D. vegeta	0	—
Homeria elegans × Homeria miniata	Many	Healthy not yet flowered
Freesia muirii × Anomatheca viridis (Lapeirousia)	0	—
Anomatheca viridis (Lapeirousia) × Freesia muirii	0	—
Anomatheca juncea (Lapeirousia) × Freesia refracta	0	—
Geissorhiza heterostyla × Gladiolus fasciculatus	0	—
Gladiolus fasciculatus × Geissorhiza heterostyla	0	—
Schizostylis coccinea × Hesperantha falcata	Several	No germination
Dierama pendulum × Sparaxis elegans	0	—
Sparaxis elegans × Dierama pendulum	0	—
Gladiolus fasciculatus × Anomalesia cunonia	Many	Healthy not yet flowered
Anomalesia cunonia × Anomalesia saccatus (Kentrosiphon)	Many	Viable seed
Gladiolus cardinalis × Gladiolus buckerveldii (Petamenes)	Many	Healthy seedlings
Gladiolus buckerveldii (Petamenes) × Gladiolus cardinalis	0	—

4. DISCUSSION

The cytology, cytotaxonomy and possible phylogeny of the genera.

The cytological or strictly speaking karyological observations can be discussed at two levels. Firstly, at the family level where it can be seen that the genera of the Iridaceae fall into natural groups based on general chromosome morphology and secondly, at the generic level where in most cases, genera or small groups of genera, have similar karyotypes. Morphological and karyological features can frequently be linked so that the most significant characters for classification can be recognised. In this way generic relationships are often indicated, and subtribes can be distinguished. Phylogenetic trends are sometimes indicated and the evolution of some groups is suggested.

Two tables are provided to facilitate comparisons of cytological data in the different genera and tribes (Table 2, 3). The diploid and suggested basic number are listed for each genus and the chromosomes have been divided arbitrarily into size categories to show similarities and differences in length.

4.1 THE CLASSIFICATION AT SUBFAMILY LEVEL AS SUGGESTED BY THE CYTOLOGY

It can be seen from cytological observations that there are two recognisable series of karyotypes. One group has relatively large chromosomes, which under the treatment described, range from 4 to 10μ, though sometimes smaller, and the other group has small chromosomes ranging from 1 to 5μ. This appears to be significant as there is a strong correlation between these karyotypic groups and the major subdivisions of the family proposed by various authors.

All the genera of the tribe *Moraeeae* (sensu Bentham & Hooker) belong to the group with long chromosomes. Of the fifteen genera in this tribe, twelve have been cytologically examined, at least to a small extent and all have large chromosomes.

Short chromosomes are found in all the genera of the Ixieae (sensu Bentham & Hooker) that have been examined. Since Bentham & Hooker, the concept of this tribe has altered only a little in that some members of the *Crocoideae* were placed here by Lewis. At present the number of genera in the tribe is 36 and all but four have been cytologically studied. Although cytological evidence does partly support Lewis in placing the *Crocoideae* in this tribe, *Crocus*, one of the genera involved, proves to be the exception in the tribe in having many species with long chromosomes. This appears to be anomalous and suggests that *Crocus* is perhaps misplaced in the classification. There is, however, some evidence that the large chromosomes may be a specialised condition in *Crocus* and this will be discussed fully under the section on *Romulea* and its allies.

The *Sisyrinchieae* of Bentham & Hooker is an unnatural group and even as modified by Lewis, who removed the *Crocoideae* from here, it remains rather heterogeneous. There are about 20 genera in this group and unfortunately only eight have been cytologically investigated. The chromosomes are small and in those species studied by the present author, are as small as the smallest chromosomes in the *Ixieae*. One exception is *Bobartia*, placed in the subtribe *Sisyrinchiineae* (previously *Eusisyrinchieae*). It has rather large chromosomes and its present position requires further elucidation.

The *Sisyrinchieae* have been altered in concept by Weimarck and further by Lewis who removed the *Crocoideae* to the *Ixieae*. In its modified composition it contains genera which are the least specialised in the family. The rootstock is a rhizome, the leaves are unmodified and the inflorescences usually much branched with regular flowers which only rarely have a perianth tube. Cheadle

(1964) who investigated the xylem elements in the family, found that *Aristea* and its allies were in this respect by far the least specialised. Thus a large part of this group can be regarded as primitive and it should be placed at the beginning of the classification.

There has not been sufficient cytological study of the *Sisyrinchieae* to enable the cytological data to be used to evaluate its taxonomic circumscription. Most of the few genera examined have small chromosomes and are clearly distinct from the *Moraeeae* so that the treatment of Pax, who merged the *Sisyrinchieae* and *Moraeeae* together in a single subfamily, cannot be supported. At the present state of our knowledge, the *Sisyrinchieae* should be maintained as a single tribe, though perhaps it may be found to consist of two or more groups of equal rank with the *Moraeeae* and *Ixieae*, as did Hutchinson.

TABLE 2

The karyotypic features of genera in the tribes *Sisyrinchieae* and *Irideae* studied by the present author. Somatic number, a suggested basic number and the relative length of the chromosomes are shown.

Genus	Somatic No. 2n	Suggested Basic No. x	Description		
			Long = >4μ	Med.	Short = <2,5μ
Tribe SISYRINCHIEAE					
Aristea	32, 64	16	—	—	16
Klattia	32	16	—	—	16
Nivenia	32	16	—	—	16
Patersonia	24	12	—	1	11
Witsenia	32	16	—	—	16
Bobartia	20	10	4	6	—
Tribe IRIDEAE					
Dietes	20, 40	10	7	3	—
Ferraria	20, 60	10	5	5	—
Moraea	20, 24, 18, 12	10	7	3	—
Gynandriris	12	6	6	—	—
Galaxia	16, 32	8	5	3	—
Homeria	12, 24, 36	6	6	—	—
Hexaglottis	12, 10	6	6	—	—

The genera which require study for the understanding of *Sisyrinchieae* are mainly South American, but a few are Australasian. Until these are satisfactorily examined, none of the existing subdivisions of this tribe can be validated.

The *Moraeeae* appear to be a natural group and should be maintained as the second major group in the family. According to the code of botanical nomenclature the name of a taxon below family rank must be derived from the same stem as the next higher taxon when it contains the type of this taxon. Consequently, *Moraeeae* is illegitimate and the name *Irideae* as substituted by Lewis must be followed. As this group is somewhat specialised it should not be placed at the beginning of the classification but rather after the *Sisyrinchieae*.

TABLE 3

The karyotypic features of genera of the tribe *Ixieae*. Somatic number, a suggested basic number and relative length of the chromosomes are shown.

Genus	Somatic No. 2n	Suggested Basic No. x	Description		
			Long = $>4\mu$	Med.	Short $<2{,}5\mu$
Tribe IXIEAE					
Pillansia	44	11	—	—	11
Thereianthus	20	10	—	1	9
Micranthus	20	10	—	1	9
Watsonia	18, 27	9	—	2	7
Tritoniopsis	32	16	—	—	16
Anapalina	34	17	—	—	17
Lapeirousia	20, ?18	10	1	—	9
Anomatheca	22	11	—	1	10
Freesia	22	11	—	1	10
Schizostylis	26	13	—	—	13
Hesperantha	26	13	—	—	13
Geissorhiza	26, 39, 52	13	—	—	13
Engysiphon	26	13	—	—	13
Melasphaerula	22	11	—	—	11
Gladiolus	30, 45, 60	15	—	—	15
Acidanthera	30	15	—	—	15
Radinosiphon	30	15	—	—	15
Homoglossum (including Petamenes)	30	15	—	—	15
Anomalesia	30	15	—	—	15
Romulea	32–18, 44, 54	12	—	—	12
Syringodea	12, 22	6	—	2	4
Dierama	20	10	—	2	8
Ixia	20, 40	10	—	2	8
Sparaxis	20	10	—	2	8
Synnotia	20	10	—	2	8
Tritonia	22, 44	11	—	2	9
Crocosmia (including Curtonus)	22	11	—	2	9
Chasmanthe	20	10	—	2	8
Antholyza (including Anaclanthe)	14	7	2	1	4
Babiana	14	7	2	1	4

Hutchinson's treatment which divides the *Irideae* into three tribes is not convenient as the relationship among the genera in these tribes is then obscured. In this respect the Bentham & Hooker system is better, although the genera within this single unit could perhaps be grouped naturally into subtribes following Hutchinson's subdivisions. The inclusion by Pax of the *Cipureae* of Bentham & Hooker in this group cannot be commented upon, for none of the genera have been cytologically investigated.

The *Ixieae* are also a natural group both morphologically and cytologically and except for Hutchinson, who divided the group into three equal ranking tribes, has been regarded as a single entity. Hutchinson's treatment is artificial

for it results in the placing of related genera with similar karyotypes in different tribes. Clearly the *Ixieae* must remain as one of the major groupings within the family. Bentham & Hooker's treatment must, however, be modified to include the *Croceae* as Lewis proposed. The genera of the *Ixieae* have, with one exception, a cormous rootstock, the inflorescence is usually a spike and in several genera extremely zygomorphic flowers are found. On these grounds the tribe is considered to contain the most specialised plants in the family and should be placed last in the classification, as was done by Bentham & Hooker.

4.2 Tribe 1. *SISYRINCHIEAE.*

The *Sisyrinchieae* comprises plants with the least specialised rootstocks in the family, these being either unmodified or rhizomatous. The leaves are of the equitant type, the flowers are arranged in cymose clusters and are generally fugaceous and actinomorphic. The stamens are alternate to the style branches or lobes.

Cytotaxonomy and possible phylogeny.

Subtribe 1. ***Aristeineae.***

Aristea, *Patersonia*, *Nivenia*, *Witsenia* and *Klattia*.

This group consists of relatively unspecialised plants with an unmodified rootstock or a rhizome. The South African representatives of the group, as well as the Australian genus, *Patersonia*, are dealt with. The group comprises both herbaceous and woody or shrubby plants, the latter being *Nivenia*, *Witsenia* and *Klattia*. The flowers are unspecialised, actinomorphic and the style is undivided.

ARISTEA

2n = 32, 64.

This genus comprising about fifty species is distributed widely over sub-Saharan Africa and in Madagascar, occurring in montane regions in the tropics, but in the lowlands as well in the temperate south, where the largest number of species is found. The plants are typically herbaceous, blue flowered and lack a perianth tube.

Twelve of the approximately fifty species were examined cytologically. (Table 4). In all but two species the diploid number of 32 was obtained. One population of *A. glauca* and the South African form of *A. ecklonii* were found to be polyploid, having a somatic number of 64. In all cases the chromosomes are very small and often difficult to examine. Little size difference is noticeable, all chromosomes being from 1 to 5μ long. Most of the chromosomes are acrocentric though occasionally sub-metacentric ones can be distinguished. Satellites were seen only rarely but in *A. bicolor* two were observed. No idiogram has been compiled owing to the great similarity of the chromosomes. (fig. 1).

There have been only two previous chromosome counts in this genus (Table 4). Fernandes & Neves (1961) found a somatic number of approximately 65 in *A. ecklonii* while Riley (1962) reported a diploid number of 32 in *A. major*. In the present work the count for *A. major* is confirmed and somatic numbers of 32 and 64 were found in different populations of *A. ecklonii*. It appears that the plant studied by Fernandes & Neves was a polyploid and probably had 64 chromosomes.

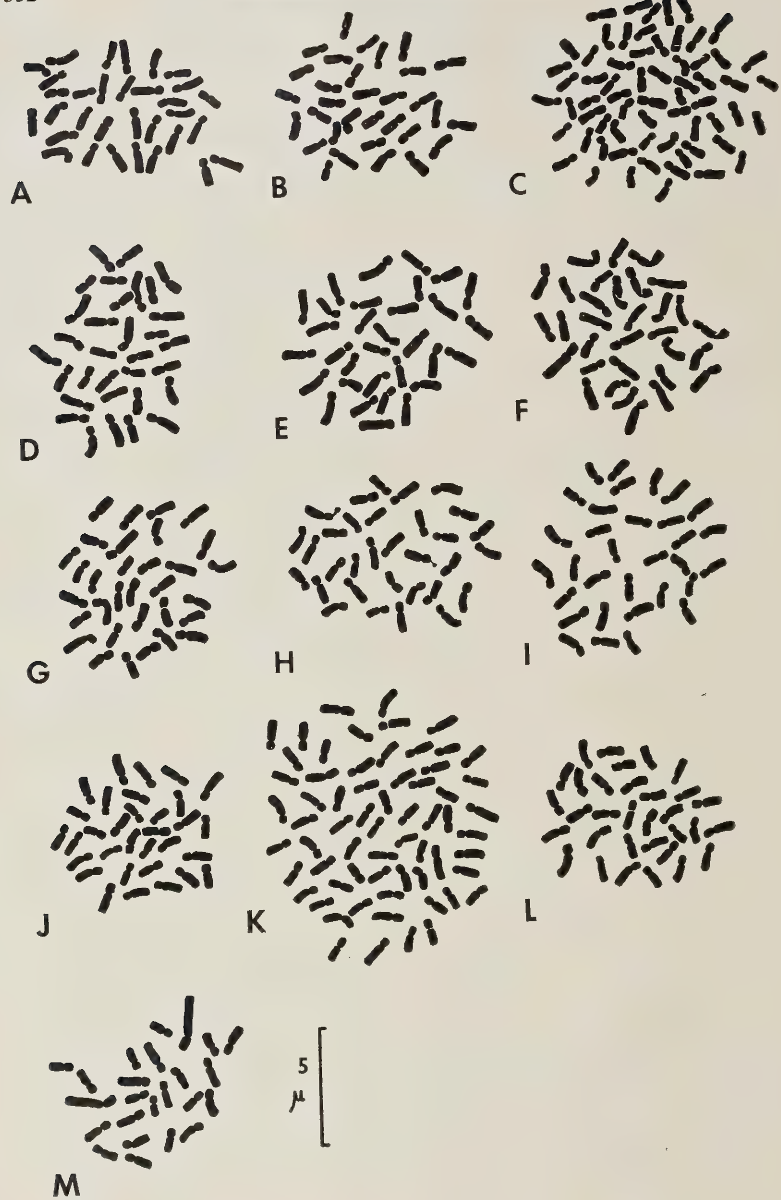
TABLE 4

Chromosome numbers in *Aristea, Patersonia, Nivenia, Witsenia, Klattia* and *Bobartia*.

Species	Diploid No.	Collection Data or Reference
ARISTEA Ait.		
A. woodii N. E. Br.	32	Sabie, Tvl. *Goldblatt 81* (*J*)
A. ecklonii Bak.	64	Haenertsburg, Tvl. *Goldblatt 3* (*J*)
	±65	(Fernandes & Neves 1961)
A. ecklonii Bak. var.	32	Chimanimani Mountains, Rhodesia *Goldblatt 151, 164* (*J*)
A. confusa Goldblatt (=capitata)	32	Kalk Bay, C.P. *Goldblatt 416*
A. major Andr. (=thyrsiflora)	32	Constantia, C.P. *Goldblatt 399*
(as thyrsiflora)	32	(Riley 1962)
A. spiralis (L.f.) Ker.	32	Klein River Mnts., C.P. *Goldblatt 418*
A. monticola Goldblatt (=A. coerulea)	32	Ceres, C.P. *Goldblatt 401*
A. biflora Weimarck	32	Caledon, C.P. *Goldblatt 215*
A. juncifolia Bak.	32	Cape Point Reserve, C.P. *Goldblatt 480*
A. africana (L.) Hoffmg.	32	Steenberg Plateau, C.P. *Goldblatt 182*
A. glauca Klatt.	32	Cape Point Reserve, C.P. *Goldblatt 396*
	64	Kenilworth, Cape Town, C.P. *Goldblatt 398*
PATERSONIA R. Br.		
P. occidentalis R. Br.	24	Perth (Australia), seed from Kings Park
NIVENIA Vent.		
N. levynsiae Weimarck	32	Buffelstaalberg, Rooi Els, C.P. *Goldblatt 464*
N. stokoei (Guthrie) N. E. Br.	32	Betty's Bay, C.P. *Goldblatt 407*
N. corymbosa (Ker) Bak.	32	Bains Kloof, C.P. *Goldblatt 185*
WITSENIA Thunb.		
W. maura Thunb.	32	Betty's Bay, C.P. *Goldblatt 407*
KLATTIA Bak.		
K. partita Bak.	32	Kogelberg, C.P. *Rourke 1186* (NBG)
BOBARTIA L.		
B. lilacina Lewis	20	Donker Kloof, Du Toit's Pass, C.P. *Esterhuysen 32376*
B. gladiata (L.f.) Ker.	20	Bains Kloof, C.P. *Goldblatt 412*
B. indica L.	20	Silvermine, C.P. *Goldblatt 400*

All localities given are in South Africa unless otherwise stated. Provinces are abbreviated as follows: Cape Province – C.P.; Transvaal – Tvl. Specimens are housed in the Bolus Herbarium, Cape Town, unless stated to the contrary.

The chromosome counts for the other eight species studied in this work are new records. Of these, all but one proved to have a diploid number of 32.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The exception is a polyploid form of *A. glauca* with 64 chromosomes. It is clear that with about a quarter of the species in the genus having been investigated, the basic number of *Aristea* is 16.

Polyploidy in *Aristea*

Aristea ecklonii is an unusual species for it clearly has both polyploid and diploid races. All three geographically separate populations sampled by the author in South Africa, from the Transvaal to the eastern Cape Province, proved to be polyploid, while a Rhodesian population was diploid. Plants of the latter population were somewhat different morphologically from the southern ones, having much longer seed capsules. It is likely that the Rhodesian plants belong to a separate sub-species. The occurrence of polyploidy in *A. glauca* is also problematic. Two separate populations on the Cape Peninsula were studied and one proved diploid and the other polyploid. In view of the rarity of polyploidy in the Iridaceae in the south western Cape Province, it seems likely that the polyploid population is abnormal and may be a case of isolated autopolyploidy. The problem does, however, require further investigation.

PATERSONIA

$2n = 24$.

This is an Australian genus which appears to be allied to *Aristea*. It has a similar habit and vegetatic appearance, has blue to purple flowers but differs in having reduced or absent inner perianth segments. Only one species was examined. The chromosomes are comparatively small but there is a single pair of long chromosomes which give the karyotype a distinctive appearance. The chromosomes of this species are acrocentric and similar in appearance and size to *Aristea* except for the presence of the large pair of chromosomes (fig. 1:M).

NIVENIA

$2n = 32$.

Nivenia, together with *Witsenia* and *Klattia* comprise the so called woody or shrubby genera of the Iridaceae. They all have rather woody stems, lack modified rootstocks and exhibit secondary growth. *Nivenia* appears to be the least specialised of the group, having blue flowers and resembling *Aristea* in many ways. The flowers differ in having a short perianth tube.

Nivenia comprises eight species, three of which were examined cytologically by the author. All have a similar karyotype in which the diploid number is 32. The chromosomes are all acrocentric and small, ranging in size from 1 to 2μ.

FIG. 1.

Karyotypes of *Aristea* and *Patersonia*. A. *Aristea woodii;* B. *A. ecklonii;* C. *A. ecklonii* var.; D. *A. confusa;* E. *A. major;* F. *A. spiralis;* G. *A. monticola;* H. *A. bicolor;* I. *A. juncifolia;* J. *A. africana;* K, L. *A. glauca;* M. *Patersonia occidentalis.*

The chromosomes are very slightly larger than those found in species of *Aristea*, but except for this, the karyotypes are remarkably similar (fig. 2, A, B, C).

WITSENIA

2n = 32.

Witsenia is a monotypic genus found in the south western Cape Province. Although a woody plant, it is found only in marshy places that are moist all year round. *Witsenia maura* has a diploid number of 32. The karyotype is very similar to that of *Nivenia* and *Aristea* both in the size and general appearance of the chromosomes (fig. 2:D).

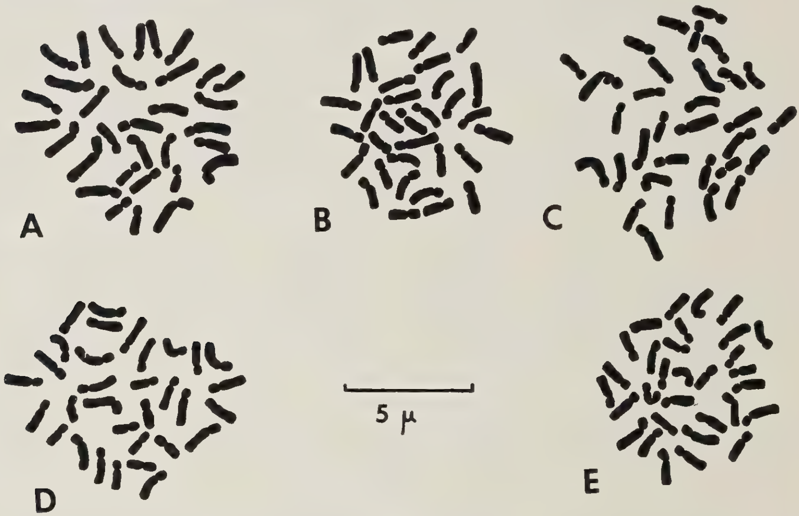

FIG. 2.

Karyotypes of *Nivenia, Witsenia* and *Klattia*. A. *Nivenia levynsiae;* B. *N. stokoei;* C. *N. corymbosa;* D. *Witsenia maura;* E. *Klattia partita.*

KLATTIA

2n = 32.

Klattia the third of the woody genera, is also confined to the south western Cape. There are two species in the genus, both found at fairly high altitudes in the mountains where the rainfall is fairly high. The flowers on the shrubby plants seem rather specialised. They are enclosed in the large brightly coloured bracts, and only the stamens and style appear beyond the bracts.

Only one of the two species, *Klattia partita* was studied. The diploid number is 32 and the karyotype is very similar to those of *Witsenia, Nivenia* and *Aristea* (fig. 2:E).

There have been no previous cytological reports on the above four genera. It is clear that the woody South African genera, *Nivenia*, *Klattia* and *Witsenia* have a basic number of 16 and have a karyotype very like that of *Aristea*. *Patersonia occidentalis*, the Australian species, has quite a different karyotype, but seems to share with *Aristea* and the other genera of the group a general similarity in the size and appearance of the chromosomes. This can perhaps be taken as evidence of its relationship to the South African genera, though probably this is rather distant.

The classification of *Aristea* and its allies.

Aristea and *Patersonia* have usually been treated as belonging to the same tribe or subtribe (Bentham & Hooker 1883). The woody or shrubby genera have been accorded the same treatment until recently, and in fact *Nivenia* was regarded as belonging to *Aristea* by Bentham & Hooker and Hutchinson. In his revision of *Aristea*, Weimarck (1940) discussed the systematic position of *Aristea* and its allies and concluded that the shrubby genera, *Patersonia* and others, were sufficiently distinct in having a perianth tube to be placed in a separate tribe from *Aristea* which he placed in the *Sisyrinchieae* (sensu Hutchinson). As Weimarck was following Bentham & Hooker's classification, he removed *Nivenia*, *Witsenia* and *Klattia* from the tribe *Aristeae* and placed them in the new tribe *Nivenieae* together with *Patersonia* and several South American genera. Lewis (1954) continued to recognise the woody genera as distinct and placed them alone in the *Nivenieae*, one of the three tribes she recognised, while referring *Aristea* to the tribe *Irideae* with *Homeria*, *Moraea* and their allies.

The cytological results do not support the treatments of either Weimarck or Lewis for it appears that *Aristea* and the woody genera form a natural unit and although *Patersonia* appears allied to this group it is more distantly related. The classification of Bentham & Hooker and of Hutchinson, who modified it only slightly, is generally in accord with the cytological evidence. Pax's treatment, however, seems the best for he placed *Aristea* and the woody genera in one subtribe and *Patersonia* in the other subtribe of the *Aristeae*.

As similarity in karyotype is evidence of genetic and consequently phylogenetic relationship it seems that no classification is tenable that does not recognise the relationship of *Aristea* to the woody genera. If the shrubby habit and secondary growth are regarded as justification for referring the woody genera to a distinct group then *Aristea* must be recognised as constituting a similar monotypic group of equal rank.

Weimarck's system would have *Aristea* in the *Sisyrinchieae*, while *Nivenia* etc. with the same karyotype as *Aristea*, are in another tribe. Lewis' system is untenable for the same reason. It appears then that Weimarck's reason for

breaking up the old subtribe *Aristeae* on the basis of presence or absence of a perianth tube is not a good one, and that the perianth tube is not a character of great significance. The feature of secondary growth and shrubby habit used by Lewis in separating *Nivenia* and *Aristea* is also clearly not one of sufficient importance for the maintenance of the *Nivenieae* as a distinct tribe. *Aristea* and the shrubby genera must be admitted to the same tribe or subtribe but below this level it is only a matter of opinion whether further subdivision should be made to separate *Aristea* from the woody genera on the basis of presence or absence of secondary growth.

A study of the xylem elements in the Iridaceae by Cheadle (1964) is very significant, for the tribe *Aristeae* (*Aristea*, *Nivenia*, *Klattia* and *Patersonia*) was found to have the most primitive vessels in the family. Vessels are only found in the roots of Iridaceae except for *Sisyrinchium* and vary in length and nature of their perforation plates. Most of the family have specialised vessels but the *Aristeae* are the exception. This confirms the suggestion of other taxonomists that *Aristea* and its allies are the most primitive group in the family. The grouping of *Aristea*, the woody genera and *Patersonia* is also supported, while Weimarck's placing of *Aristea* with *Sisyrinchium* is shown to be incorrect.

Hence the cytological and anatomical evidence supports the maintenance of *Aristea*, the woody genera, and *Patersonia* in a single group. It is proposed that together with the South American genera which appear to be morphologically allied, they be placed in a single subtribe of the *Sisyrinchieae*, called the *Aristeineae*.

The occurrence of secondary growth in the *Monocotyledonae* is unusual, but is known in several genera. It was found by Scott & Brebnor (1893) and Adamson (1926) that secondary growth in *Nivenia*, *Klattia* and *Witsenia* resembled that found in other *Monocotyledonae*. The phylogenetic significance of the feature is not known. It was once regarded as the remnant of the primitive condition in the *Monocotyledonae* but can as equally be regarded as a secondary specialisation.

The geographical distribution of the woody genera is reminiscent of old relict populations for they occur in isolated groups on mountains, ravines or in marshes. They do not, however, appear to be primitive for they have rather specialised inflorescences and, except for *Klattia*, have flowers with a perianth tube. In view of the primitive nature of the vessels in these genera they cannot be regarded as very advanced, but are perhaps more specialised than *Aristea* from which they may have been derived.

Subtribe 2. ***Sisyrinchiineae***.

Only African representative: *Bobartia*.

This group is more specialised than the *Aristeineae*, having a rhizome, sometimes a modified, terete leaf and flowers with divided style branches.

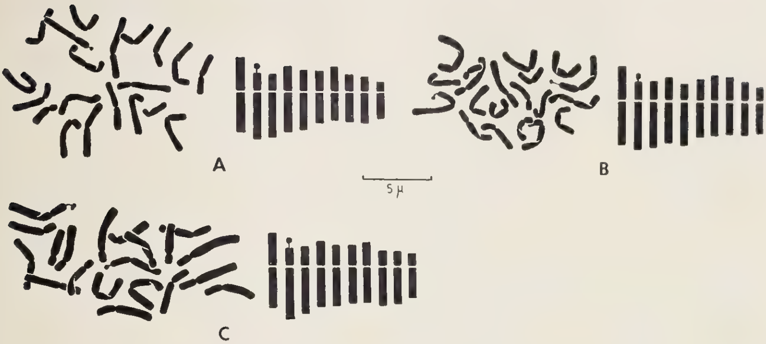

FIG. 3.
Karyotypes and idiograms of *Bobartia*. A. *Bobartia lilacina;* B. *B. gladiata;* C. *B. indica.*

BOBARTIA

Bobartia is a fairly small genus of about twelve species found throughout the winter rainfall region of the Cape Province. The plants are herbaceous, and possess a creeping, rhizomatous rootstock. The flowers have a short perianth tube, equal segments, and have a divided, three branched style. Typically, the flowers are yellow though one species has blue flowers.

Three species were studied by the author (Table 4). In all three a similar karyotype with a diploid number of 20 was found (fig. 3). The chromosomes are considerably larger than those found in *Aristea* and its allies and range in size from about 3—5 μ. The chromosomes are of sufficient size for details of the karyotype to be clearly visible and idiograms for all three species could be constructed. As can be seen in fig. 3, the karyotypes are remarkably similar. The longest chromosome pair is metacentric in all three species and the second longest pair bears a small satellite at the end of the shorter arm of the chromosome.

There are two distinct growth forms in the genus. Two species have a narrowly ensiform leaf and a much ramified paniculate inflorescence. One of the species studied here, *B. lilacina*, has this habit (Lewis 1945). A peculiarity of these two species is the presence of a sticky material found below each node of the aerial part of the plant. This feature occurs in the tribe *Irideae* in a few species of several genera, e.g. *Moraea*, *Homeria* and *Ferraria.*

The other type of growth form in *Bobartia* is clearly more specialised. The leaves are linear or terete, and the inflorescence condensed so that the scape is unbranched and the flowers grouped in a compact head. It has been suggested that the two growth forms are so different that *Bobartia* should be divided into

two genera on these grounds. While there is some merit in the argument, the floral morphology is very similar in both groups. The cytology is similar in both, and confirms that they are closely related. It is more a question of convenience as to whether the genus should be divided. Because the genus is small, and the two unusual branched species can be very easily recognised, it does not seem necessary to alter their present taxonomic treatment.

Bobartia belongs to the tribe *Sisyrinchieae* which, as already mentioned, characteristically has small chromosomes. Though *Bobartia* at first seems to prove an exception, a closer examination of the general chromosome size in this genus as compared with species in the *Irideae* shows that chromosomes are more slender and significantly smaller than, for example, in *Dietes* where a diploid number of 20 is also found. *Bobartia* appears to be intermediate between the small and large chromosome groups. The difference in chromosome size between it and the remainder of the genera in the *Sisyrinchieae* that have been studied seems significant and *Bobartia* is clearly only distantly related to *Aristea* and its allies.

The anatomy of the xylem elements has been mentioned in the section on *Aristea* where it was shown that *Aristea* and its allies have the most primitive vessels in the family. *Bobartia* does not belong to this group for it has the relatively specialised vessels typical of the rest of the family. In *Sisyrinchium*, suggested by some authors to be a close ally of *Bobartia*, specialised xylem vessels occur in aerial parts of the plant as well as the roots. This genus is anatomically the most specialised in the family, but there is no indication that *Bobartia* has any vessels in its stems and leaves.

Morphologically *Bobartia* and *Sisyrinchium* appear intermediate between the *Aristea* group and the *Irideae*. In both the rootstock is a rhizome, the leaves equitant and usually ensiform and the inflorescence consists of a number of small cymes (or rhipidia) each containing two usually fugaceous flowers enclosed in large bracts or spathes. The main difference between the groups is that the flower usually has a perianth tube in *Aristeineae* (but not in *Aristea*) and the style is always undivided, but in the *Sisyrinchieae*, the perianth tube is always absent and the style is divided into 3 long branches. In some genera of the *Irideae*, the vegetative features are similar but the flowers have a branched style with forked or divided stigmas and, more significant, they have the style branches opposite the stamens and not alternate as in the rest of the family. Apart from this, the *Irideae* have very large chromosomes which serve to emphasise the distinctness of this group.

As can be seen, *Bobartia* (and perhaps other members of the *Sisyrinchieae*), is to some extent intermediate between the primitive *Aristeineae* with unspecialised morphology and anatomy, and with very small chromosomes, and the more advanced *Irideae* with their more specialised flowers, and often other

modified morphological features, with very large chromosomes. If the tribe *Sisyrinchieae* is to remain recognised, *Bobartia* and *Aristea* and its allies must be placed in separate subtribes. The difference between these two subtribes does, however, seem greater than between the other subtribes that are recognised by the present author, and perhaps *Aristea* and *Bobartia* should be placed in separate tribes. More genera in the *Sisyrinchieae* (sensu lato) should be examined recognise two tribes here and until then *Bobartia* should be placed in the subtribe *Sisyrinchieae*.

4.3 Tribe 2. *IRIDEAE*

The tribe *Irideae* comprises plants often more modified than the *Sisyrinchieae*. The rootstock is either a rhizome, bulb or corm and the leaves equitant or secondarily bifacial. The inflorescence, a cyme, enclosed in large spathe-like bracts, is similar as is the fugaceous habit of the flowers. These are, however, often modified by reduction or difference of the inner perianth segments and the style and style branches are usually elaborate. The tribe is world wide in distribution, the best known genus being *Iris*. The African genera are *Dietes*, *Moraea*, *Gynandriris*, *Homeria*, *Hexaglottis*, *Galaxia* and *Ferraria*.

THE CYTOLOGY, CYTOTAXONOMY AND POSSIBLE PHYLOGENY OF THE SOUTH AFRICAN GENERA.

a. The genus ***Dietes***

$2n = 20, 40.$

Dietes comprises about six species of fairly large herbaceous plants. The rootstock is a woody, creeping rhizome, the leaves long, equitant and firm and the inflorescence a tall, fairly branched structure bearing clusters of flowers at the apices of the branches. The flowers are similar to those of *Iris* with large outer and smaller inner perianth segments and a large petaloid and branched style. The flowers differ in lacking a perianth tube and the inner segments are spreading and not erect as in most species of *Iris*. The genus has a peculiar distribution in that five species occur along the south east coast of Africa while the sixth is found in eastern Australia and Lord Howe Island.

The cytology of four of the six recognised species was investigated (Table 5). In three, *Dietes vegeta*, *D. grandiflora* and *D. butcheriana*, a diploid number of 20 was obtained, but *D. bicolor*, with a somatic number of 40 appears to be polyploid. The karyotypes of all the species are fairly similar and are characterised by having several metacentric chromosomes (fig. 4: A—F). This is perhaps closest of all the genera studied by the author to the symmetric karyotype of Stebbins (1950), in which there are several metacentric chromosomes, and no great difference in size occurs between the chromosomes. This karyotype is frequently correlated with primitive characters and is believed to be less specialised than the asymmetric karyotype in which acrocentric chromosomes occur.

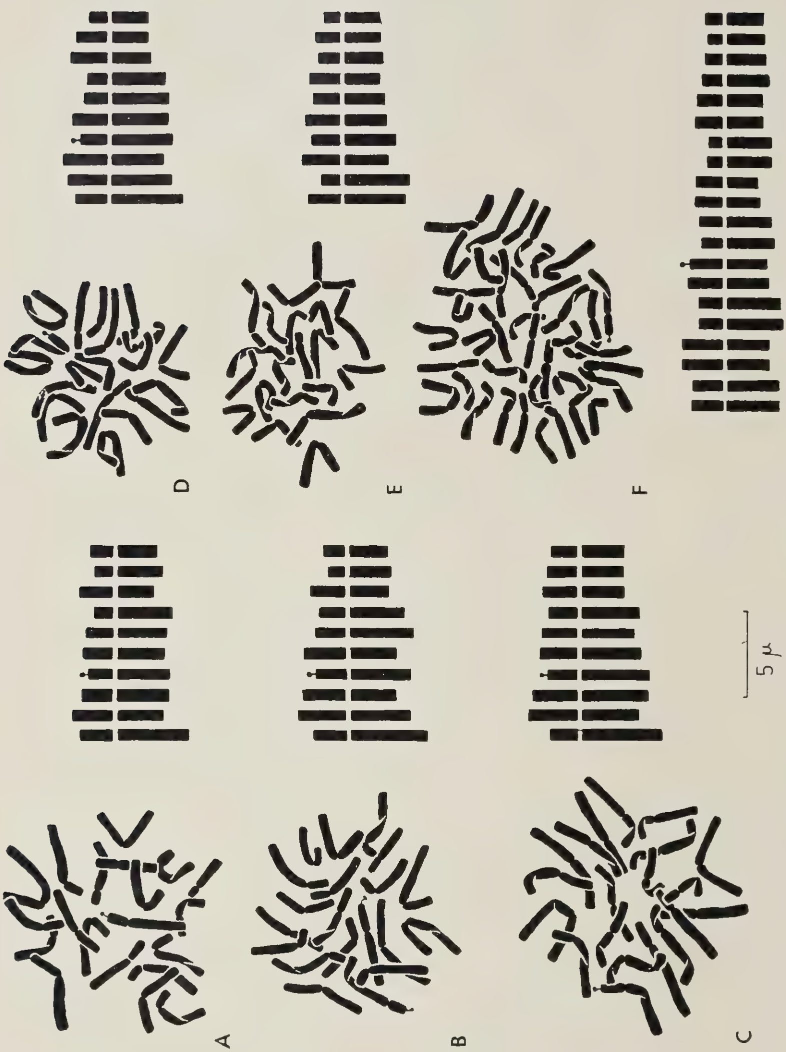

FIG. 4.

Karyotypes and Idiograms of *Dietes*. A. *Dietes vegeta* from Inanda, Natal; B. *D. vegeta* from Inhaca Island; C. *D. vegeta* from Haenertsburg; D. *D. grandiflora*; E. *D. butcheriana*; F. *D. bicolor*.

Three separate geographical races of *Dietes vegeta* were examined. In the past these three types were recognised as two different species and a variety (Brown 1928) but are now considered a single species (Obermeyer 1969). The karyotypes of the geographical races were found to vary little, and resembled one another more closely than those of the other species studied (fig. 4: A, B, C). This degree of intraspecific variation in the karyotype is to be expected in widely separate populations or races and tends to confirm the placing of these in a single species.

The present study confirms the finding of Sharma & Sharma (1960) and Sakai (1952) who obtained a diploid number of 20 in *Dietes vegeta* (known to them as *Moraea iridioides* var. *johnsonii*). Riley (1962) also reported a diploid number of 20 in this species (as *D. prolongata*). The karyotypes found by these workers appear to be similar to those found by the present author and fit within the limits of karyotypic variation for *D. vegeta.*

TABLE 5
Chromosome numbers in *Dietes* and *Gynandriris*.

Species	Diploid No.	Collection Data or Reference
DIETES		
D. vegeta (L.) N.E. Br. . . .	20	Inanda, Natal. *Mauve 4443* (PRE)
	20	Inhaca, Mocambique. *Goldblatt 91* (J)
	20	Haenertsburg, Tvl. *Goldblatt 381.*
(as Moraea iridioides var. johnsonii)	20	(Sakai 1952)
(as D. iridioides var. johnsonii)	20	(Sharma & Sharma 1960)
(as D. iridioides var. mcleyii) .	40	(Sharma & Sharma 1960)
(as D. prolongata)	20	(Riley 1962)
D. grandiflora N.E. Br. . . .	20	Natal (ex. hort) *Goldblatt 46* (J)
D. butcheriana Gerstner . . .	20	Noodsberg, Natal. *Strey 4875* (PRE)
D. bicolor (Lindl.) Sweet . .	40	Eastern Cape (ex. hort.) *Goldblatt 35* (J)
(as D. iridioides var. bicolor) .	40	(Sharma & Sharma 1960)
GYNANDRIRIS		
G. sisyrinchium (L.) Parl. . .	24	Europe (Simonet 1932)
G. setifolia (L.f.) Foster . . .	12	Villiersdorp-Worcester Rd., C.P. *Goldblatt 208.*
G. torta (L. Bol.) Foster . . .	12	Nieuwoudtville, C.P. *Goldblatt 273.*

All localities given are in South Africa unless otherwise stated. Provinces are abbreviated as follows: Cape Province – C.P.; Transvaal – Tvl. Specimens are housed at the Bolus Herbarium unless stated to the contrary.

Sharma & Sharma also reported finding a diploid number of 40 for both *Moraea iridioides* var. *mcleyii* (presumably a horticultural variety of *Dietes vegeta*) and *M. iridioides* var. *bicolor* (*D. bicolor*). This latter count is confirmed by the present study. *Dietes bicolor* seems to be a tetraploid species, and apparently an allopolyploid, as the chromosomes can be matched in pairs but not in fours. Meiosis in this species was examined and found to be normal

and all the plants examined were fully fertile. On the assumption that the species is allopolyploid, an attempt was made to discover its ancestry by crossing it with *D. vegeta*, the only species which occurs in the same natural locality. A cross between *D. bicolor* and *Moraea ramosissima* a species with a similar karyotype was also attempted but both crosses proved unsuccessful.

The chromosome counts for *D. grandiflora* and *D. butcheriana* are new records and tend to confirm the suggestion that the basic number for *Dietes* is 10.

The taxonomic position and phylogenetic significance of *Dietes*.

Dietes is a genus belonging to the tribe *Irideae* and it has the long chromosomes typical of this group. The distribution of the genus is peculiar as five of the species occur in southern Africa from the Cape Province to Malawi and the remaining species is found in southern Queensland and on Lord Howe Island off the east coast of Australia. *Dietes* is allied to *Iris* and *Moraea* and has been included within both genera at one time or another. It was considered by Baker (1896) and Cahen (1943) to be a subgenus of *Moraea*. The latter author suggested that the recognition of *Dietes* as a genus on the grounds of its rhizomatous rootstock, would be inconsistent with the treatment accorded to *Iris*. Cahen had, however, an incomplete understanding of *Dietes* and did not realise it differed in other respects from *Moraea*. The present author believes that *Dietes* is intermediate between *Iris* and *Moraea* and cannot thus be correctly incorporated within either genus. It shares with them the characteristic double-crested petaloid style branches but it also has a number of features which can be regarded as more primitive than those in *Iris* and *Moraea*: the rootstock is a creeping rhizome; the leaves are equitant; the scape very ramified and the flowers have spreading perianth segments, no perianth tube and free stamens (fig. 5: A).

Iris and *Moraea* have diverged from this basic type in two directions. The rootstock in *Iris* has remained a rhizome or has been modified to form a bulb, the branching is reduced and the flowers have a perianth tube. In the bulbous species of *Iris* the leaf has also become modified and is bifacial with only the apex equitant. In *Moraea* the rootstock is a corm, the branching is reduced in many species and while the flower has no perianth tube (except in a single species), the filaments in most species are connate and form a column round the base of the style. The leaves in *Moraea* are bifacial but in many species the apex is

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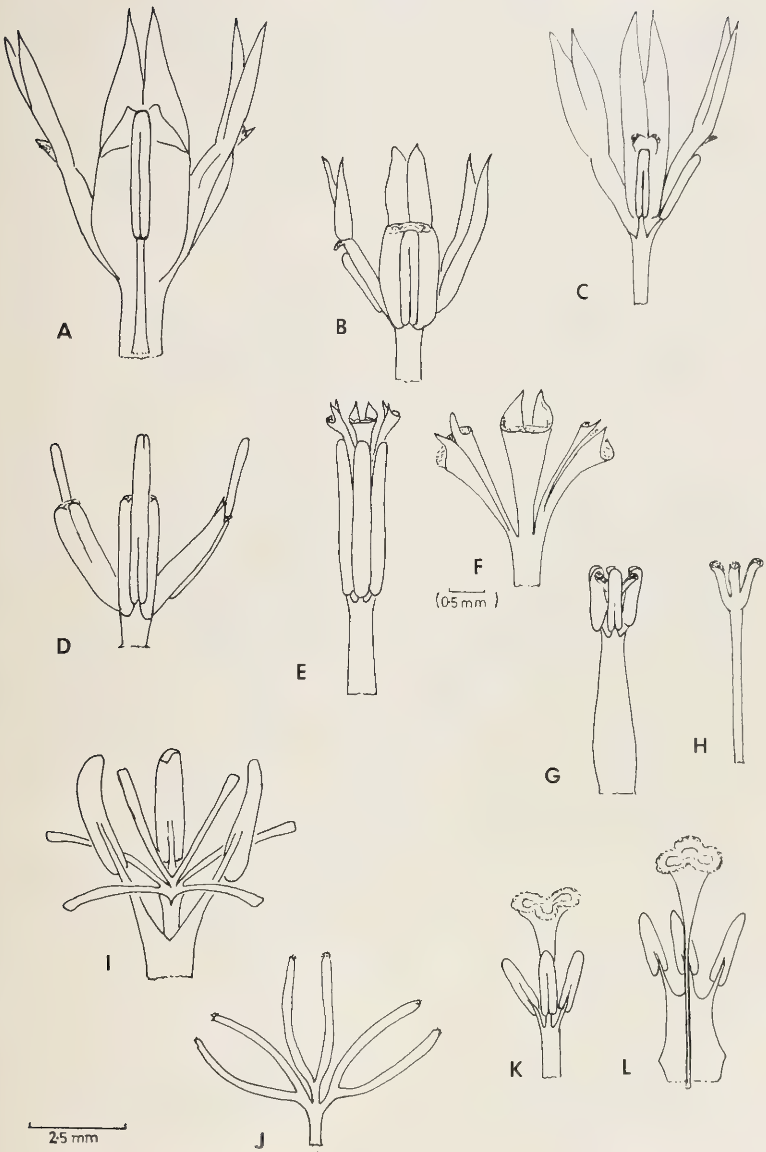
FIG. 5.

The structure and arrangement of the stamens, style and stigma in the South African representatives of the *Irideae*. A. *Dietes vegeta;* B. *Moraea macronyx;* C. *M. villosa;* D. *M. gigandra;* E. *Homeria breyniana;* F. *H. breyniana* with style partly dissected; G. *H. miniata;* H. *H. miniata* style with stamens removed; I. *Hexaglottis virgata;* J. *H. sp.* showing style branches in detail; K. *Galaxia ovata;* L. *G. ovata* partly dissected.


A
B
C
D
E
F
(0·5 mm)
G
H
I
J
K
L
2·5 mm

equitant. It is believed that the so-called leaf is in this case an extended leaf sheath, which explains its bifacial nature and the equitant tip would thus be the vestigial remains of the true leaf (Arber 1921, Lewis 1954).

Iris is widely distributed throughout the northern hemisphere while *Moraea* is an African genus occurring mainly south of the equator with the greatest concentration of species in the south western Cape Province. It is believed that the two genera developed independently in different areas, but apparently from a common ancestor very like *Dietes* if not that genus itself. If this theory is correct it would be expected that the basic or primary chromosome number in both *Moraea* and *Iris* would be 10. Diploid numbers of 20 do in fact occur in these genera, both of which are heteroploid. The idea that this number is primitive may prove helpful in unravelling complexities of evolution in *Iris* and *Moraea*.

b. The genus ***Moraea***

$2n = 12, 18, 20, 24.$

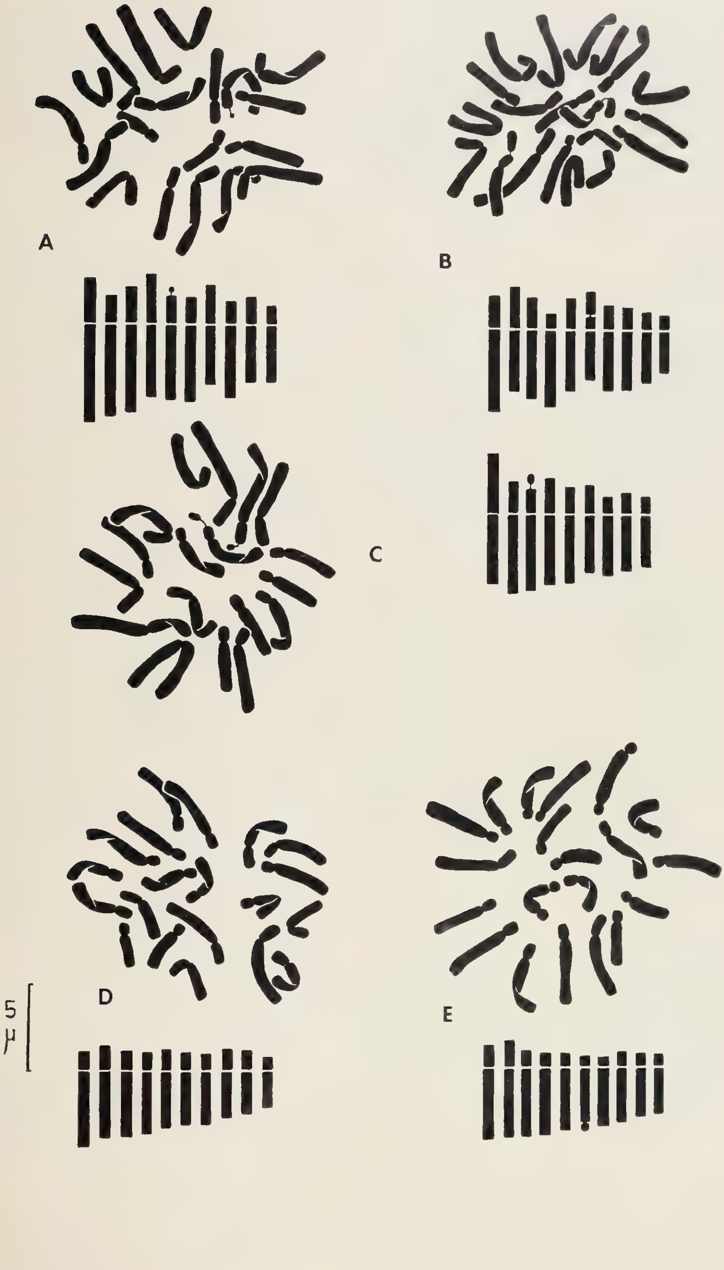
The genus *Moraea* is a comparatively large one, comprising an estimated 60 species. The genus is distributed throughout sub-Saharan Africa with increasing frequency southwards; the greatest concentration of species being in the south western Cape Province. The plants are herbaceous and usually quite small. The rootstock is a corm consisting of an enlarged lateral bud and the leaves are bifacial instead of the usual monofacial type found in the family. The flowers are much like those of *Iris* and have large petaloid styles, the difference being that *Moraea* generally lacks a perianth tube and the filaments are contiguous and usually connate.

Twenty-five species, which reflect a fairly large sample of the total number, were studied by the present author. Large chromosomes were found in all species, but considerable variation in karyotype was observed. Diploid numbers of 20 and 12 are most common with 18 and 24 also occurring.

The species that were examined have been arranged after the system of Baker (1896) and as can be seen, different diploid numbers are sometimes observed in the same section. (Table 7). This is probably indicative of certain errors in the system. The karyotypes of the species will be discussed briefly as idiograms are given for each species and these give a more accurate impression of each karyotype than a verbal description. For purposes of comparison, the species are discussed in groups having similar karyotypes and not according to Baker's system.

Fig. 6.

Karyotypes and idiograms of *Moraea*. A. *Moraea ramosissima;* B. *M. odorata;* C. *M. papilionacea;* D. *M. neglecta;* E. *M. angusta.*


A
B
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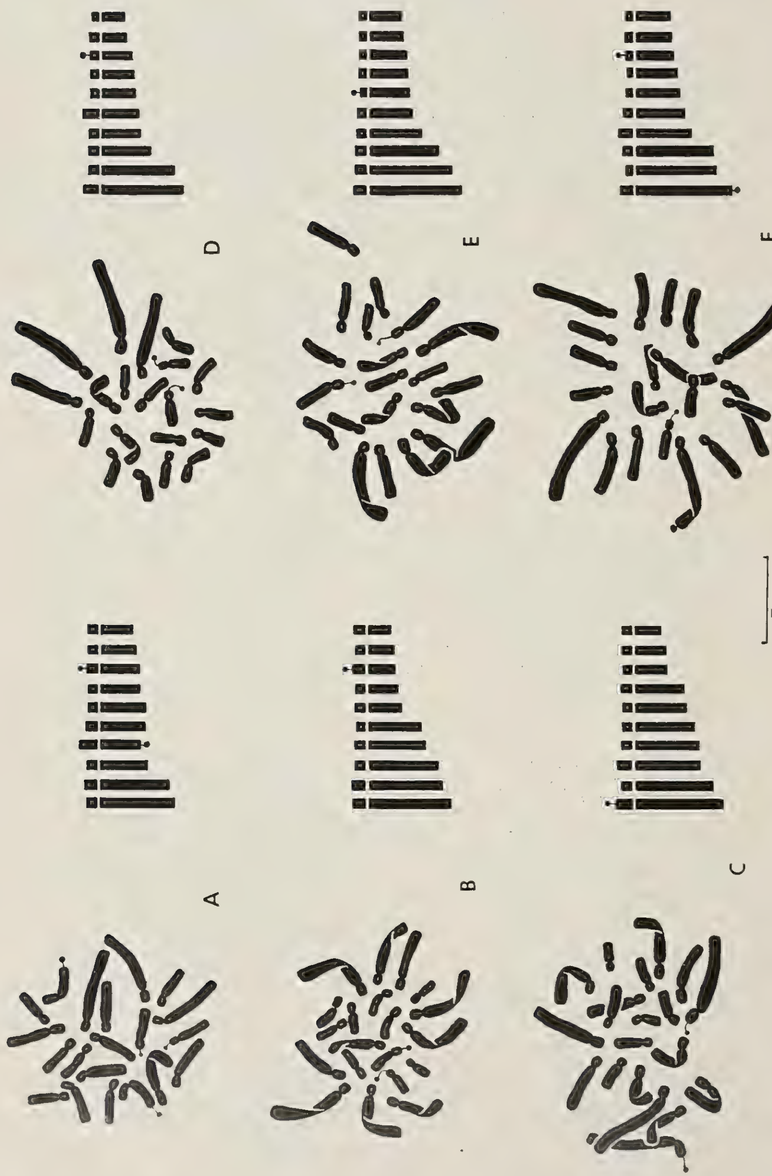


FIG. 7.
Karyotypes and idiograms of *Moraea*. A. *Moraea cooperi*; B. *M. framesii*; C. *M. juncea*; D. *M. gawleri*; E. *M. ciliata*; F. *M. macronyx*.

Of the species with a diploid number of 20, *M. ramosissima* and *M. odorata* appear to have the least specialised karyotypes if the view of Stebbins (1950) is accepted that the symmetrical karyotype with many metacentric chromosomes is primitive and unspecialised (fig. 6: A, B). In both species the variation in size is comparatively less than other species with 20 somatic chromosomes and there are two pairs of metacentric chromosomes in *M. odorata* and three in *M. ramosissima*.

The diploid number is 20 in *M. angusta* and its close ally *M. neglecta*, but here the karyotype is less symmetrical for there is a greater range in size and there are no metacentric chromosomes (fig. 6: D, E).

Moraea cooperi, *M. juncea*, *M. framesii*, *M. gawleri*, *M. ciliata* and *M. macronyx*, all having a diploid number of 20 appear to form a natural unit judging from the karyotype which is quite asymmetric here (fig. 7). All the chromosomes are acrocentric and there is considerable difference in size between the large and small chromosomes. The difference is least in *M. cooperi* which appears intermediate between this group and *M. angusta* in its karyotype. The remaining five species with this asymmetrical karyotype have chromosomes of similar sizes and have three or four pairs of larger chromosomes and the remaining pairs quite small. They differ, however, in having satellites on different pairs of chromosomes.

Moraea papilionacea seems unique in having a diploid number of 18 but it appears to be related to the species with the rather symmetric karyotype with 20 somatic chromosomes (fig. 6: C). The karyotype in this species is also rather symmetrical with a pair of metacentric and several pairs of submetacentric chromosomes.

The species with 12 or 24 chromosomes can also be divided into groups with symmetric and asymmetric karyotypes. *Moraea diphylla*, *M. fugax*, *M. insolens*, *M. polystachya*, *M. tripetala* and *M. trita* (apparently a tetraploid) all have at least one pair of almost metacentric chromosomes as in *M. polystachya* and even four pairs as in *M. diphylla* (fig. 8). There is no very great similarity in any of the karyotypes, as can be seen from the different positions of the satellites, the number of metacentric chromosomes and the variation in size, which is small in *M. polystachya* but considerable in *M. fugax*.

Moraea lurida, *M. bellendenii* and *M. villosa* all have karyotypes comparable to those of the previous group (fig. 11: A, B, C). *M. villosa* seems to be a polyploid species. Three geographically isolated populations were examined and all were found to have a somatic number of 24. The above three species are mentioned separately as they belong to a group accorded subgeneric rank by Baker. In these species the longest chromosome is conspicuously metacentric and at least in *M. bellendenii* and *M. villosa* can be seen to bear a small satellite at its one end.

Fig. 8.
Karyotypes and idiograms of *Moraea*. A. *Moraea diphylla*; B. *M. fugax*; C. *M. insolens*; D. *M. trita*; E. *M. tripetala*; F. *M. polystachya*.

FIG. 9.

Karyotypes and idiograms of the *Moraea spathulata* complex. A. *Moraea spathulata* from Harrismith, O.F.S.; B. *M. spathulata* from Graskop, Transvaal; C. *M. spathulata* from Knysna, Cape Province; D. *M. sp. aff. moggii* from Lochiel, Transvaal.

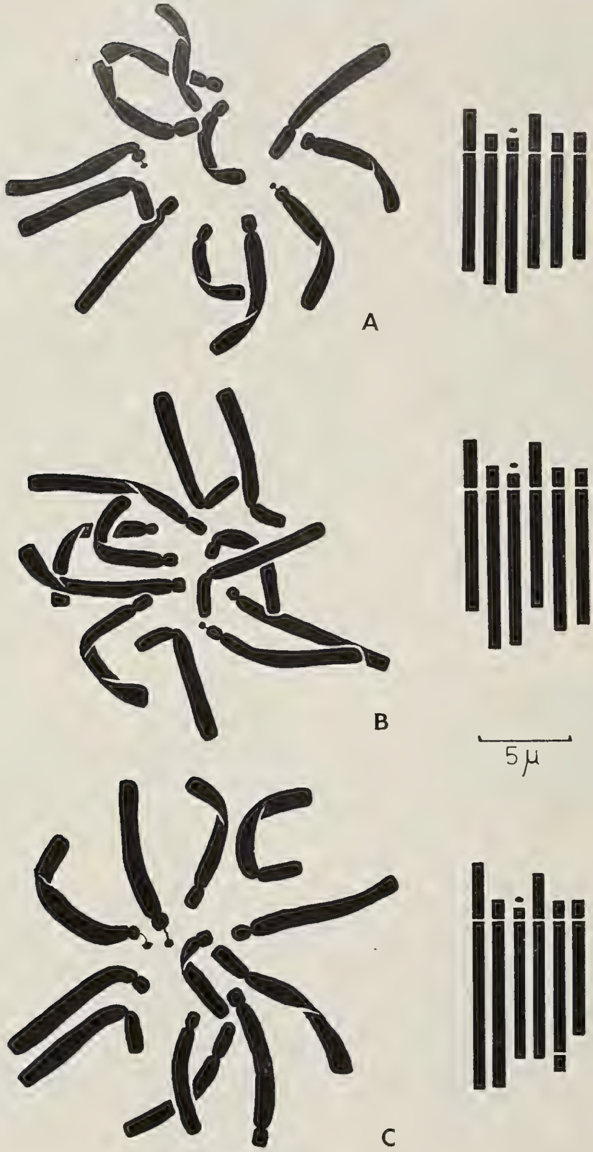


FIG. 10.
Karyotypes of *Moraea*. A. *Moraea rivularis;* B. *M. graminicola;* C. *M. schimperi.*

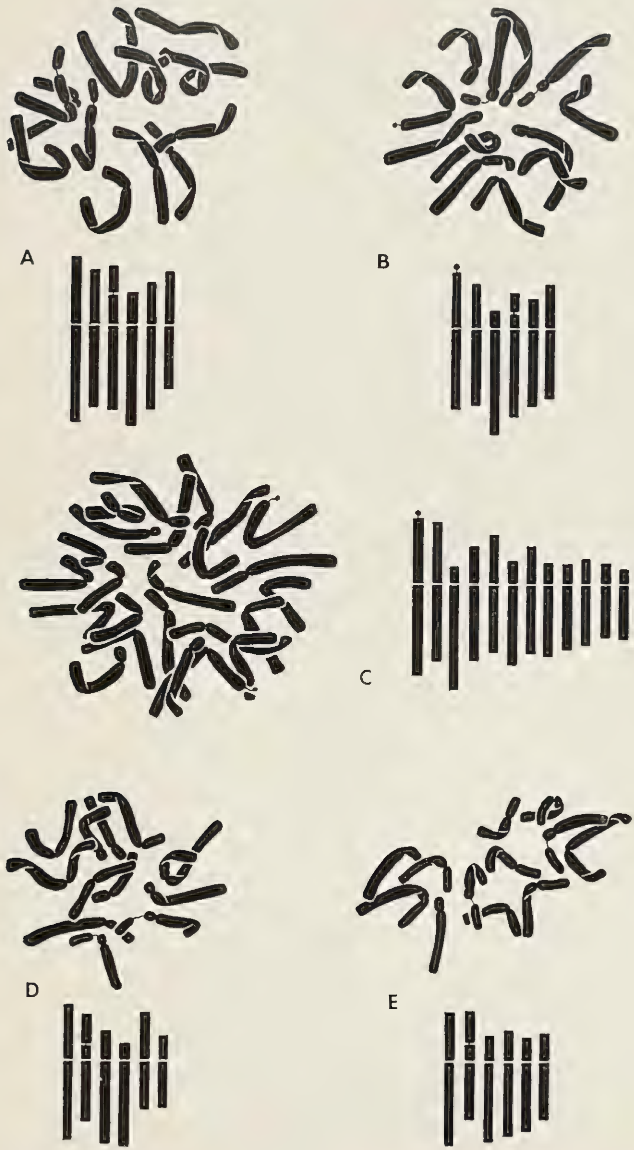


FIG. 11.
Karyotypes and idiograms of *Moraea* and *Gynandriris*. A. *Moraea lurida;* B. *M. bellendenii;* C. *M. villosa;* D. *Gynandriris setifolia;* E. *G. torta.*

The remaining species, *M. spathulata* and its allies, with 12 chromosomes all have a very similar karyotype. The chromosomes are very large and mostly acrocentric (fig. 9, 10). The longest and fourth longest pair are submetacentric and the third longest pair bear a small satellite at the end of the shorter arm. *M. spathulata* is itself a very widespread species extending from George in the Cape Province to the northern Transvaal. Three populations were examined from different areas and all were found to have a similar, but to a small extent different karyotype. It seems that small variations in karyotype do occur in species and may not have taxonomic significance. A similar conclusion was reached by Pienaar (1963) for the genus *Ornithogalum*.

There have been several earlier cytological reports on species of *Moraea*. Sakai (1952) reported a diploid number of 20 in *M. ramosissima* and 28 in *M. fugax* (as *M. edulis*). The first is confirmed by the present author although a rather different karyotype was recorded. The second count is, however, quite different from present observations and it is suggested that a mistake in identification of Sakai's plant was made. Fernandes and Neves (1961) reported a diploid number of 20 in *M. juncea* and Riley (1962) found 12 somatic chromosomes in *M. polystachya* and *M. spathulata*. These reports are confirmed by the present author. Lewis (1966) found a diploid number of 12 in both *M. erici-rosenii* and *M. spathacea*, and described the karyotypes as similar to that found by Riley for *M. spathulata*. These species have not been examined by the present author as they were not available. Apart from the five counts confirmed by the present author, there are 20 new cytological records for the genus.

The correlation of cytology and morphology.

The species of *Moraea* having a diploid number of 20 can be divided into three groups based on morphological criteria. The first group which corresponds to the section *Corymbosae* (subgenus *Moraea*) according to Baker (1896), consists of the plants which have a much ramified inflorescence and bear from three to several basal leaves. The karyotype in this group varies to some extent, ranging from that of *M. ramosissima* with rather large chromosomes, several of which are metacentric to *M. decussata* where an asymmetrical karyotype with both large and rather small acrocentric chromosomes occur.

The second group, corresponding to Baker's section *Acaules* comprises rather reduced species where the stem is unbranched and is rather short and enclosed by the three to several basal leaves. Only two of the five species in this section, *M. ciliata* and *M. macronyx*, were examined and these were found to have a karyotype very much like *M. juncea* and *M. gawleri*, both belonging to the previous section, *Corymbosae*. These latter two species are small and *M. juncea* particularly, has a short stem and few branches. It can thus be

TABLE 6

Chromosome numbers in *Moraea*. The arrangement and classification are after Baker (1896.)

Species	Diploid No.	Collection Data or Reference.
Subgenus 1. Moraea		
Section Corymbosae		
M. ramosissima (L.f.) Druce . .	20	Stellenbosch, C.P. *Goldblatt 50* (J)
	20	(Sakai 1952)
M. odorata Lewis	20	Quoin Point, C.P. *Goldblatt 478*
M. cooperi Bak.	20	Caledon district, C.P. *Goldblatt 440*
M. juncea L.	20	Groot Constantia, C.P. *Goldblatt 474*
	20	(Fernandes & Neves 1961)
M. framesii L. Bolus	20	Van Rhyns Pass, C.P. *Goldblatt 270*
M. gawleri Spreng (=decussata, or crispa)	20	Cape Point Reserve, C.P. *Goldblatt 502*
M. polystachya (Thunb.) Ker .	12	Beaufort West, C.P. *Goldblatt 88 (J)*
	12	Graaff Reinet, C.P. *Goldblatt 221*
	12	(Riley 1962)
Section Acaules		
M. ciliata (L.f.) Ker	20	Nieuwoudtville, C.P. *Goldblatt 256*
M. macronyx Lewis	20	Calvinia district (ex hort) 144 (J)
Section Brevicaules		
M. papilionacea (L.f.) Ker . .	18	Tulbagh Rd., C.P. *Goldblatt 193*
	18	Constantia Nek, C.P. *Goldblatt 445*
Section Monocephalae		
M. angusta (Thunb.) Ker . .	20	Malmesbury Rd., C.P. *Goldblatt 444*
M. neglecta Lewis	20	Elim, C.P. *Goldblatt 361*
M. spathulata (L.f.) Klatt . .	12	Harrismith, O.F.S. *Naude s.n.* (*PRE 30038*)
	12	Graskop, Tvl. *Goldblatt 14 (J)*
	12	Knysna, C.P. *Goldblatt 26 (J)*
	12	(Riley 1962)
(as M. spathacea)	12	(Lewis 1966)
M. sp. aff. moggii N. E. Br. . .	12	Lochiel, Tvl. *Goldblatt 86 (J)*
M. erici-rosenii	12	(Lewis 1966)
M. graminicola Oberm. . . .	12	Mooi River, Natal. *Mauve 4466* (PRE)
M. schimperi (Hochst) Pichi Sermolli	12	Nyika Plateau, Malawi. *Goldblatt 40 (J)*
M. lurida Ker	12	Klein Hagelkraal, C.P. *Goldblatt 363*
Section Subracemosae		
M. diphylla Bak.	12	Giftberg, C.P. *Goldblatt 207*
M. fugax (de la Roche) . . .	12	Hopefield, C.P. *Goldblatt 152* (J)
Jacq. (=M. edulis)		
(as M. edulis)	28	(Sakai 1952)
M. trita N. E. Br.	24	Johannesburg, Tvl. *Goldblatt 155*
Subgenus 2. Vieusseuxia		
M. insolens Goldblatt ined. . .	12	Caledon, C.P. *Barnard s.n.* (NBG 87509)
M. bellendenii (Sweet) . . .	12	Napier, C.P. *Goldblatt 338*
M. villosa Ker	24	Tulbagh, C.P. *Goldblatt 22*
	24	Riebeeck Kasteel, C.P. *Goldblatt 503*
M. tripetala (L.f.) Ker . . .	12	Nieuwoudtville, C.P. *Goldblatt 101*

All localities given are in South Africa unless otherwise stated. Provinces are abbreviated as follows: Cape Province—C.P., Transvaal—Tvl. Specimens are housed at the Bolus Herbarium unless stated to the contrary.

suggested that there is a tendency for reduction in size and branching in the *Corymbosae* which leads through *M. juncea* to the *Acaules*. The relationship between this group and the smaller members of the *Corymbosae* is evidenced by the similarity of the karyotype.

The third group of species of *Moraea* with a diploid number of 20 consists of *M. angusta* and *M. neglecta*. These are also apparently modified from the *Corymbosae* but here the aerial stem is well developed and the branching is reduced and usually absent. The number of leaves is fewer, and there is often only a single basal leaf. These two species were placed by Baker in the section *Monocephalae* characterised by an unbranched stem with a terminal cluster of flowers. The remaining species that he referred to in this group were found to have a diploid number of 12.

Only one species, *M. papilionacea* was found to have a diploid number of 18. This and *M. fimbriata* (not examined) comprise Baker's section *Brevicaules*, characterised by plants with short but branching stems and several basal leaves. The karyotype of *M. papilionacea* seems to be most similar to *M. ramosissima* in size and appearance of the chromosomes but of course there is a reduction in number. *Moraea papilionacea* appears to be allied to the *Corymbosae* but may be a link between that group and the species of *Moraea* having a diploid number of 12.

Those species of *Moraea* with 12 or 24 somatic chromosomes can also be divided into groups based on their morphology. The first of these corresponds to Baker's section *Subracemosae* which comprises plants with two, or more often, only one basal leaf and stem bearing only a few short branches. In this group, which includes *M. fugax*, *M. diphylla* etc., the karyotype is characterised by having one or two metacentric chromosomes.

A second group is the remainder of Baker's *Monocephalae*. As characterised by *M. spathulata*, these species have a single leaf and unbranched inflorescence. Here the karyotype seems more asymmetric than in the previous group for there are no metacentric chromosomes. As is so often observed, the asymmetry of the karyotype is associated with morphological specialisation and species in this group are clearly among the most reduced or modified in the genus.

The third group with a base number of 6 corresponds to Baker's separate subgenus, *Vieusseuxia*. In this group the vegetative features seem to be relatively specialised for there are only one or two leaves and the stem is little branched. The group was given subgeneric status because of the modification of the flower. The inner perianth segments are very small and often tricuspidate or sometimes almost vestigial. Here the karyotype consists of rather large chromosomes, several of which are metacentric.

The value of the criteria on which Baker based this last group appears rather doubtful. *Moraea cooperi* ($2n = 20$), placed in error by Baker in the *Corymbosae*

(according to his criteria), actually lacks inner perianth segments and should thus be considered as belonging to the subgenus *Vieusseuxia*. Clearly the plant would be misplaced here for it is much branched and the karyotype is like that in other members of the *Corymbosae* where it should remain, though this group must be redefined.

The *Moraea tripetala* was one species included in *Vieusseuxia* by Baker because it had very reduced inner perianth segments. It is perhaps misplaced here as it is unlike most other members of this subgenus which usually have very broad, oval outer segments and tricuspidate inner segments. The reduction of the inner segments in *M. tripetala* may be an independent change comparable to that in *M. cooperi* which is clearly well placed in the section *Corymbosae*. The outer perianth segments in *M. tripetala* are lanceolate with a raised midline and down-turned edges, like those in the subgenus *Moraea*. Its diploid number of 12 and moderately branched habit suggest the features of the section *Subracemosae* to which it may be better referred.

The two other subgenera of *Moraea* proposed by Baker were *Helixyra* (now *Gynandriris*) and *Dietes*, both now recognised as separate genera and treated as such by the present author. The diploid number of 20 and the much ramified habit of *Dietes* together with its rhizomatous rootstock suggest a primitive position with regard to *Moraea* where the rootstock is always a single internode corm.

Gynandriris has a cormous rootstock and a moderately branched stem. It differs from *Moraea* only in its ovary which is prolonged into a sterile upper portion or beak. Apart from this the group seems allied to the *Subracemosae* where a similar karyotype occurs.

Another species which appears misplaced in Baker's system is *M. polystachya*, referred by Baker to the *Corymbosae*. Morphologically, it is unlike most of that group for it is only little branched. As indicated by its karyotype, this vegetative habit belongs better in the *Subracemosae* where the branching is limited and a diploid number of 12 is found.

Baker's section *Monocephalae* appears to be an artificial grouping for two quite different karyotypes occur here, although morphologically the species are similar in being unbranched with a terminal inflorescence and having only a single leaf. This vegetative type may have evolved independently in the groups with 20 and 12 somatic chromosomes. There are, however, other features common to the two groups, and the most obvious of these being the nature of the seeds, which, in contrast to the round or angled seeds in the rest of the genus, are flat, disc-shaped structures with a rather spongy testa making them very light and easily distributed by the wind. The seed structure is not known in all species and the taxonomic significance of the distinctive seed needs further study. At present, however, it supports the contention that the *Monocephalae* are a natural group despite the great karyotypic variation found here.

Moraea lurida, also included by Baker in the *Monocephalae*, is clearly misplaced. It is sometimes branched and has a karyotype like that of the *Subracemosae* and *Vieusseuxia*. In the present author's opinion it is perhaps best placed in the latter group because, although the inner perianth segments are not tricuspidate or as small as in most members of the subgenus, the outer segments are the same shape, namely oval and not lanceolate. Its karyotype is perhaps closest to that of *M. bellendenii*, a member of the subgenus *Vieusseuxia*.

The origin and evolution of *Moraea*.

As postulated in the section on *Dietes*, the ancestor of the genus *Moraea* is suggested to be a plant with a much branched stem and many basal leaves. The species most resembling this are *M. odorata* and *M. ramosissima* both of which have a diploid number of 20 and which can also be regarded as having the least specialised karyotype in the genus. *Dietes*, the genus believed to be the ancestor of both *Moraea* and the related genus *Iris* also has a basic number of 10 with several species having 20 somatic chromosomes and a karyotype resembling that of *M. ramosissima*.

The differences between *Dietes* and *Moraea* have been mentioned already but can be mentioned again. The rootstock is a single internode corm in *Moraea* and a creeping rhizome in *Dietes*; *Moraea* has bifacial leaves with an equitant tip while *Dietes* has equitant leaves. Though their flowers are similar in structure and have petaloid styles with bifid crests, the filaments of the stamens are usually connate in *Moraea* and free in *Dietes* (fig. 5: A, B, C).

Within *Moraea* there is very little variation in the flower structure and this is not a very useful criterion in evaluating the evolution of the group. The subgenus *Vieusseuxia* is the exception, for here several species have very short style crests, and the other species have reduced tricuspidate inner perianth segments.

The greatest variation in morphology is in the vegetative habit. As observed by Baker and confirmed by the present study there seems to be a strong correlation between the evolution of the group and a reduction in complexity of the plant body. In some cases the reduction in branching and number of leaves has been accompanied by a change in the number of chromosomes and in other cases not, but a specialisation in karyotype leading to asymmetry is repeatedly observed.

The following phylogenetic scheme is proposed for the genus. There were presumably two main lines of evolution leading from the putatively primitive much ramified type; one leading to less branched species but still with several leaves and here, the diploid number of 20 was maintained. The end of this line is the *M. ciliata* group (*Acaules*) with several leaves and no visible aerial stem. Another line leading from the basic stock is the *M. angusta* group (*Mono-*

cephalae). Here both branching and leaf number is reduced and the seeds are flattened. In this line aneuploid reduction from 20 to 12 has presumably occurred.

Another trend, also leading to less branched species with fewer or a single leaf, was presumably accompanied by aneuploid reduction leading ultimately to the diploid number of 12. *M. papilionacea* with a somatic number of 18 is probably a link in this line. This evolutionary line (*Subracemosae*) is distinct from the *Monocephalae* in that branching is not quite lost and the seeds are angled. This line may have led to the subgenus *Vieusseuxia* with its specialised flowers and the genus *Gynandriris* where the ovary is modified to form a beak. These two groups are believed to have evolved independently from the *Subracemosae*, the least specialised group in this line of evolution.

c. The genus *Gynandriris*

$2n = 12, 24.$

Gynandriris consists of about ten South African and one Mediterranean species. The species are herbaceous, corm bearing, and differ from *Moraea* only in having the ovary extended into a long sterile tube-like beak. The two species studied by the present author, *G. setifolia* and *G. torta*, both Cape species, have a diploid number of 12 (Table 5).

The karyotypes of these two species are similar and distinctive in having a rather large satellite on a pair of shorter chromosomes. Another similarity is the possession by both of an almost metacentric long chromosome (fig. 11: D, E).

The only species previously examined is *Gynandriris sisyrinchium* (as *Iris sisyrinchium*) the Mediterranean species, found by Simonet (1932) to have a somatic number of 24. In the light of the present study, this would appear to be a polyploid species. Simonet's description and illustration of the karyotype strongly supports this, as *G. sisyrinchium* has 4 long metacentric chromosomes and the 4 shortest have rather large satellites. This is remarkably like the karyotypes of both South African species studied and supports the inclusion of the Mediterranean species in this predominantly southern African genus.

Gynandriris is believed to be very closely allied to *Moraea*, in which it has frequently been included, and shares with it the very many features including the characteristic corm tunics. The difference between the genera is that *Gynandriris* has a pseudo-perianth tube formed by a sterile elongation of the ovary. This feature is unusual and can be regarded as a specialisation of the normal ovary occurring in *Moraea*. *Moraea* is a southern African genus and does not extend far beyond central Africa. *Gynandriris* shares this distribution except for *G. sisyrinchium* which extends to the Mediterranean area and eastwards into Asia as far as Afghanistan. The cytology confirms the suggested relationship between *Moraea* and *Gynandriris* and the karyotype of the latter is most similar to species of *Moraea* placed in the section *Subracemosae*.

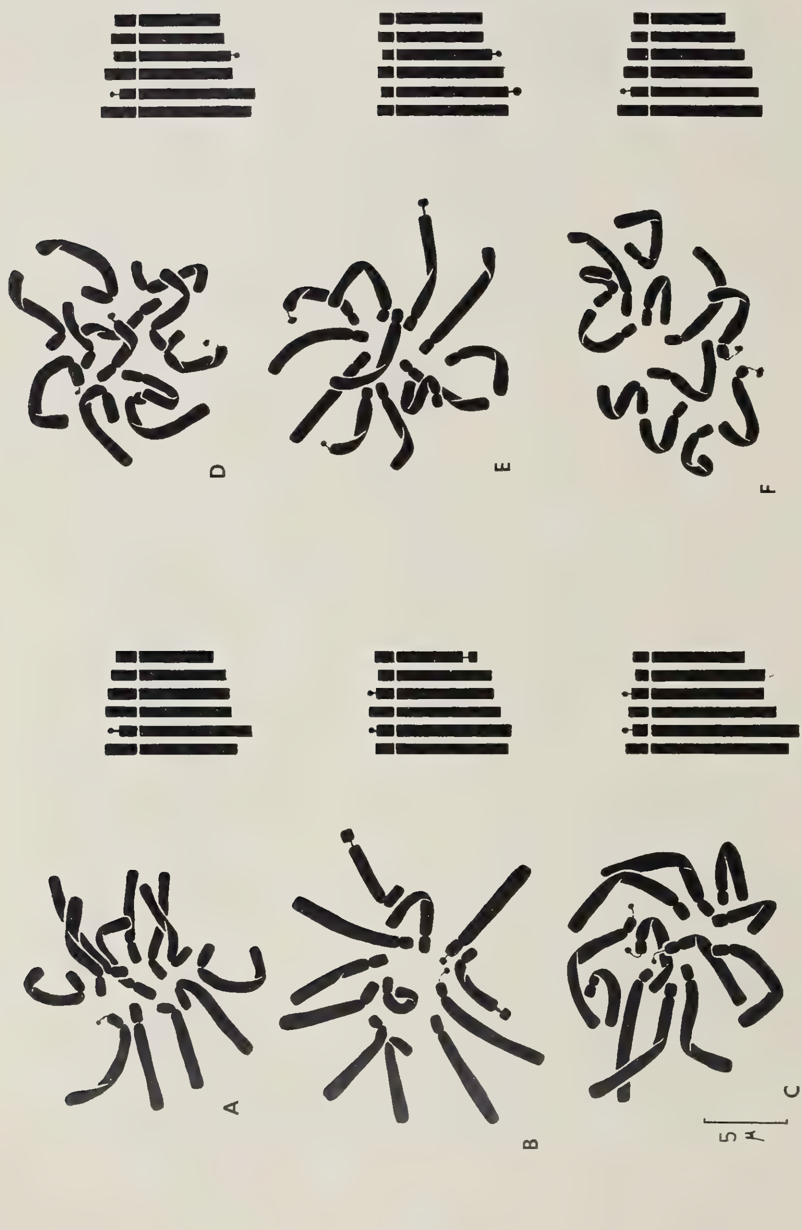


FIG. 12.
Karyotypes and idiograms of *Homeria*. A. *Homeria pura*; B. *H. ochroleuca*; C. *H. miniata*; D. *H. glauca*; E. *H. tricolor*; F. *H. papillosa*.

Fig. 13.

Karyotypes and idiograms of *Homeria*. A. *Homeria pallida*; B. *H. maculata*; C. *H. lilacina*; D. *H. breyniana*; E. *H. breyniana* var. *aurantiaca*.

In a recent classification of *Iris* (Lawrence 1953), *Gynandriris sisyrinchium* was incorporated in *Iris* again, in a section of its own. This treatment ignores the African genera *Dietes* and *Moraea* which are also closely related to *Iris*. On the criteria Lawrence uses to transfer *Gynandriris*, *Moraea* and *Dietes* must also be included in *Iris*. This would clearly be an impractical step. The alternate is to continue to recognise both *Moraea* and *Dietes* and in doing so, *Gynandriris* must be maintained as distinct, or be included in *Moraea*, the genus to which it is most closely allied according to both cytological and morphological evidence.

d. The genus ***Homeria***

2n = 12, 24, 36.

Homeria is a fairly large genus of small herbaceous plants found throughout southern Africa. It is allied to *Moraea*, having a similar corm and a bifacial leaf. The difference between the two is that *Homeria* lacks the petaloid style with the usual long crests. The perianth segments are subequal, spreading and rarely unguiculate as in *Moraea*.

Ten species and a variety of the approximately 30 species were studied here. Eight of these have a diploid number of 12 (Table 7). Two species have somatic numbers of 24 and the variety of one has 36 chromosomes. The chromosomes are large and are mostly acrocentric. Each species has its own distinctive though similar karyotype as can be seen from the illustrations (fig. 12, 13). Most species have two pairs of chromosomes bearing a satellite but there are several exceptions. One satellite is usually located on the end of the short arm of the second chromosome. In some species the satellite is on the end of the long arm of a chromosome as in *H. tricolor*. The position of the satellites is a very distinctive feature of the karyotype and together with the relative lengths of the arms of the chromosomes, gives each species its distinctive karyotype.

The polyploid species proved a little difficult to analyse and here the satellites were not seen clearly. Absence of satellites in the idiograms of polyploids probably does not mean that these plants lacked these structures but that they were more difficult to observe.

The first cytological report on *Homeria* was that of Brittingham (1934) who found a somatic number of 36 in *H. elegans*. Sakai (1952) reported a somatic number of 24 in *H. breyniana* (as *H. collina*) and a number of 36 in an unidentified species. The count for *H. breyniana* is confirmed by the present author although the karyotype illustrated by Sakai differs somewhat from that found here. Sakai found that the longest chromosome was metacentric while in the plants studied by the present author the longest chromosome is rather acrocentric. Brittingham's report for *H. elegans* is, however, not supported. It is possible that an error occurred in the identification of his plant.

Several separate populations of *H. breyniana* were examined by the present author and all proved to have 24 chromosomes. A study of meiosis in this species showed that this process was quite normal. *H. breyniana* thus appears to be an allotetraploid species. The variety of this tetraploid species proved to have 36 chromosomes. Here meiosis was also normal and var. *aurantiaca* appears to be a normal hexaploid form. The present author's opinion is that it should be regarded as a distinct species for it grows and flowers in the same localities as *H. breyniana* var. *breyniana* and is clearly reproductively isolated by virtue of its difference in ploidy.

TABLE 7

Chromosome numbers in *Homeria*, *Hexaglottis*, *Galaxia* and *Ferraria*

Species	Diploid No.	Collection Data or Reference
HOMERIA Vent.		
H. pura N. E. Br.	12	Bryanston, Johannesburg, Tvl. *Goldblatt 34* (J)
H. ochroleuca Salisb.	12	Kirstenbosch, C.P. *Goldblatt 510*
H. miniata (Andr.) Sweet	12	Garies, C.P. *Goldblatt 119* (J)
H. glauca (Wood & Evans) N. E. Br.	12	Tvl. (ex hort) *Goldblatt 95* (J)
H. tricolor L. Bol.	12	Touws River, C.P. *Goldblatt 65* (J)
H. papillosa L. Bol.	12	Van Rhyns Pass, C.P. *Goldblatt 131* (J)
H. pallida Bak.	24	Sterkstroom, C.P. *Goldblatt 67* (J)
H. elegans (Jacq.) Sweet	12	Caledon, C.P. (ex. hort) *Goldblatt 51* (J)
	24	(Brittingham 1934)
H. lilacina L. Bol.	12	Robertson, C.P. *Goldblatt 141* (J)
H. breyniana (L.) Lewis	24	Fish Hoek, C.P. *Goldblatt 507*
(as H. collina)	24	(Sakai 1952)
H. breyniana var. aurantiaca (Sweet) Bak	36	Cape Town, C.P. *Goldblatt 133* (J)
H. sp.	36	(Sakai 1952)
HEXAGLOTTIS Vent.		
H. flexuosa (L.f.) Sweet	12	Loeriesfontein, C.P. *Goldblatt 108* (J)
H. virgata (Jacq.) Sweet	10	Signal Hill, Cape Town, C.P. *Goldblatt 71* (J)
GALAXIA Thunb.		
G. citrina Lewis	16	Cold Bokkeveld, C.P. *Goldblatt 318*
G. fugacissima (L.f.) Druce	16	Rondebosch, C.P. *Goldblatt 321.*
G. c.f versicolor Lewis (flowers not seen)	16	Nieuwoudtville, C.P. *Goldblatt 311*
G. ovata Thunb.	32	Hout Bay, C.P. *Goldblatt 316.*
FERRARIA L.		
F. longa Barnes	20	Botterkloof, C.P. *Goldblatt 432*
F. undulata L.	60	Cape Town, C.P. *Goldblatt 47* (J) (ex hort)
F. cf. framesii L. Bol (flowers not seen)	20	Caledon area, C.P. (ex hort) *Goldblatt 511*

All localities given are in South Africa unless otherwise stated. Provinces are abbreviated as follows: Cape Province—C.P., Transvaal—Tvl. Specimens are housed in the Bolus Herbarium unless stated to the contrary.

Homeria pallida, the other polyploid, is a widespread species occurring in the summer rainfall area of the Karoo. *H. pura* (2n = 12) is considered to be synonymous with *H. pallida* by some authorities. It has a limited distribution in the Transvaal highveld and differs morphologically to some extent. The present investigation shows that the two differ in chromosome number and this, together with the morphological difference is evidence that the two should be recognised as distinct species.

Homeria appears to be a distinct and natural genus but examination reveals that it and *Moraea* differ in few aspects. In the majority of species of *Moraea* there is a marked difference between the perianth segments, for the inner are usually small and erect and the outer large and spreading. There are, however, several species which have quite large and spreading inner segments, e.g. *M. lurida* and *M. insolens*. Species with this type of perianth differ from *Homeria* only in the nature of the style which can, in both, be petaloid and bifid. In *Moraea*, however, the bifid apex or crests, extending above the stigmatic lobe, are longer than in *Homeria* where the crests are absent or shorter than the width of the stigma. Occasionally, however, the crests are fairly short in some species of *Moraea*, e.g. *M. gigandra* and here the style resembles that of *Homeria* (fig. 5: D).

Thus *Moraea* and *Homeria* seem to merge together rather indistinguishably and it is occasionally difficult to assign a species to one or the other genus. The two genera are, however, probably distinct in spite of their occasional similarities and *Homeria* must be retained if only on the grounds of convenience. The nature of the style branches remains the only good character for distinguishing these genera. In *Homeria* they are simpler and it is sometimes possible to see how this rather unusual organ is constructed (fig. 5: E, F). The crests appear to be extensions of the margins lateral to the stigmatic surface and have curved upwards to form a small erect crest. The recurved margins meet above the middle of the stigma but are fused only at the base. This structure can be seen in some species of *Homeria* (e.g. *H. marlothii*), while in *Moraea* the crests do not appear to be part of the stigma for they are quite separate from its edge (fig. 5: B, C). The style crests appear to be the continuation of the style branches and the stigmatic lobes lie on the abaxial surface of the style branch. The stigma thus appears in many *Moraeas* to be an independent extension of the lower surface of the style. This in effect means that the crests have fused with the back of the stigma. This distinction between two genera is in practice often rather difficult to see, but may help in critical species.

The phylogeny of *Homeria* is problematical. The genus can be considered as either advanced in relation to *Moraea* or primitive. If it is primitive then the seemingly less complex style and the simpler flower are easy to understand, for both these structures can be regarded as being more specialised in *Moraea*.

This hypothesis has rather disturbing consequences because *Dietes*, believed to be the ancestor of *Iris* and *Moraea*, has a rhizome and several other primtive features, but it has a petaloid style like that of *Moraea*. Thus if *Homeria* is considered to be primitive, but leading to *Moraea*, it must also be ancestral to *Dietes*. This is clearly not the case for *Homeria* has a specialised bifacial leaf and a corm and has connate stamens also found in *Moraea* but not *Dietes*.

An alternative hypothesis, that *Homeria* is phylogenetically advanced over *Moraea*, appears more tenable. In this case the bifacial leaf, connate stamens and characteristic corm found in both genera indicate close relationship and the less complex flower and style must be explained as reduction of an already modified structure. This means that those species of *Homeria* lacking style crests are the most advanced in this genus. This theory is attractive for it helps to explain the nature of the style of *Galaxia*, an obviously reduced and modified genus which has many of the features of *Homeria* but its style is reduced to a column with simple stigmatic lobes at its apex.

Other theories of the phylogeny of *Homeria* can also be suggested but apart from the previous one, only that of parallel evolution can be accepted. This would be remarkable, if correct, for the evolution of an identical corm and other vegetative modifications such as the bifacial leaf and reduction of branching would have had to occur together with the development of connate stamens and a crested sub-petaloid style.

From the cytological point of view the theory that *Homeria* is derived by simplification from *Moraea* is most acceptable. Species of *Moraea* most resembling *Homeria* in vegetative structure are those which have a basic chromosome number of 6, the same as is found in *Homeria*. These species of *Moraea* appear the most specialised in the genus, for they usually have a single leaf and few branches and their karyotype does to some extent resemble that of *Homeria*.

e. The genus ***Galaxia***

$2n = 16$.

Galaxia is a small genus of reduced plants which lack an aerial stem. The rootstock is a corm much like that found in *Moraea* and the leaves are bifacial. The scape is very reduced so that the inflorescences are subterranean and the fugaceous flowers are raised above the ground by the long perianth tube. The genus is in a state of considerable taxonomic confusion for there appear to be few characters on which to distinguish species. Although there are a large number of names in the literature, only five species seem to be recognised today. It is believed that the cytology of four distinct species was studied by the present author but owing to the difficulty with identification this may later require correction.

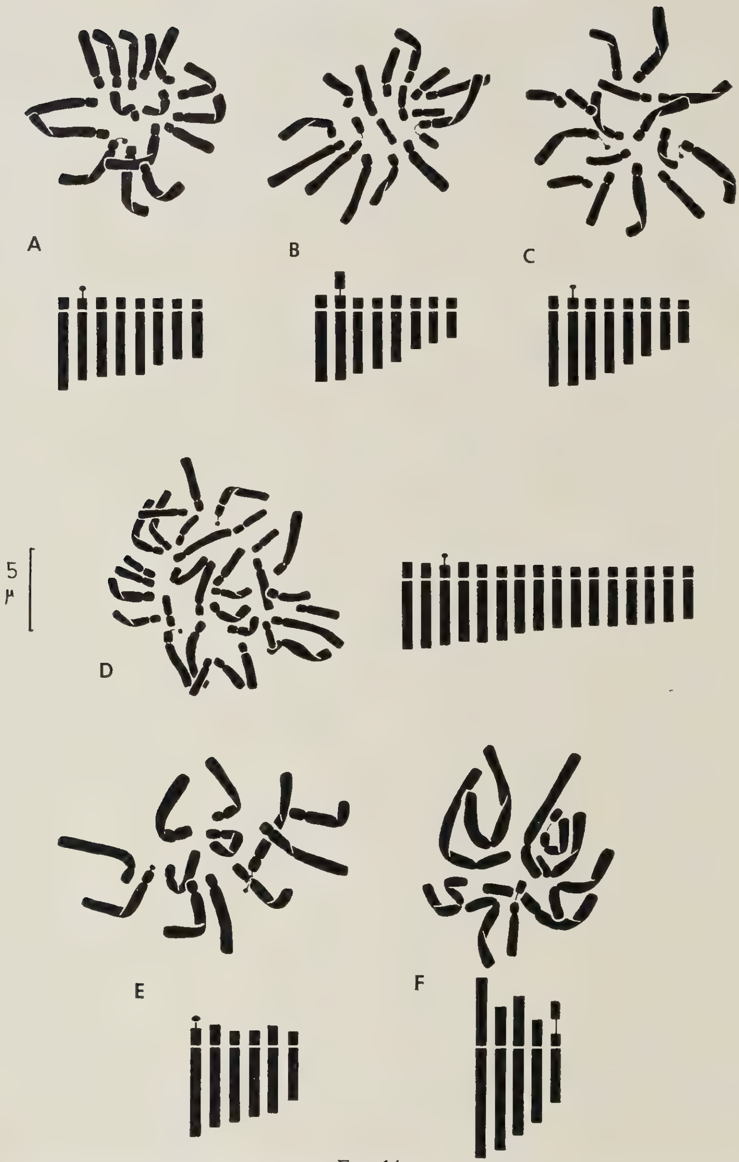


Fig. 14.
Karyotypes and idiograms of *Galaxia* and *Hexaglottis*. A. *Galaxia citrina;* B. *G. fugacissima* C. *G. cf. versicolor;* D. *G. ovata;* E. *Hexaglottis lewisae;* F. *H. virgata.*

Three species were found to have a diploid number of 16 while a plant from the Cape Peninsula, referred to *G. ovata*, proved to be polyploid with 32 somatic chromosomes (Table 7). The chromosomes are acrocentric and the second longest pair bears a satellite, which in *G. fugacissima*, is particularly large (fig. 14: A, B, C, D). The cytology of this genus has not previously been studied so the counts in this work are new records. There is a strong indication that the basic number for *Galaxia* is 8.

Galaxia is modified in a manner similar to *Syringodea* and *Crocus*, as the aerial stem is reduced and does not extend above ground level and the flowers are raised above the ground by a long perianth tube. The genus was originally classified with *Romulea*, *Syringodea* and *Crocus* in a single group but as already mentioned, Lewis (1954) showed that *Galaxia* really belonged to the *Irideae* and the other three to the *Ixieae*. This decision of Lewis has been validated by cytological study for it has the long chromosomes characteristic of this group.

Lewis believed that the genus was allied to *Homeria* for it has the type of corm found in this genus and its allies. Another feature it shares with this group is the position of the stamens which are opposite the stigmas. *Galaxia* is clearly modified for it is reduced in size, has broad bifacial leaves and the flowers are solitary as opposed to cymes in the other genera. The perianth tube also seems an advanced feature for it is not characteristic of *Homeria* and its allies. The style and stigma are simpler than in the other members of the *Irideae* and consist of a column with three expanded stigmatic lobes at the apex. If Lewis' suggestion is correct that *Galaxia* is derived from *Homeria*, which usually has a branched petaloid style, the condition in *Galaxia* has been reached by reduction and fusion of the style branches (fig. 5).

Galaxia is placed closest to *Homeria* in the *Irideae* because, like *Homeria*, it has fairly simple flowers with subequal and spreading perianth segments. The basic number in *Homeria* is 6 and that in *Galaxia* 8, which could have been derived from 6 by increasing aneuploidy. This theory of the origin of *Galaxia* has alternatives for it could easily have been derived from *Moraea* which has a more specialised flower, by reduction and simplification. Haploid numbers of 12 down to 6 occur in *Moraea* and there are reduced species in this genus though these still retain the flower typical of *Moraea*.

f. The genus ***Hexaglottis***

2n = 12, 10.

Hexaglottis is a small genus allied to *Moraea* and *Homeria*. It has the corm and bifacial leaf typical of this group. The very fugaceous flowers are actinomorphic with subequal, spreading segments. The genus is distinguished by its deeply divided style branches, which divide into two slender arms, at the ends of which are located the stigmatic surfaces.

Two of the four species in this genus were studied, both for the first time (Table 7). The diploid number for *H. flexuosa* is 12 and for *H. virgata*, 10. The chromosomes are long and the karyotype of *H. flexuosa* resembles that of *Homeria* in consisting of acrocentric chromosomes with a satellite on one of the longer pairs (fig. 14: E, F).

The karyotype of *H. virgata* is rather different for the chromosomes tend to be sub-metacentric and the longest and third chromosomes are almost metacentric. The shortest of the 5 pairs of chromosomes has an unusually large satellite. This karyotype could be described as symmetric in the terminology of Stebbins (1950) who shows that it is frequently more primitive than the asymmetric karyotype like that of *H. flexuosa*, although not necessarily so when aneuploid reduction takes place (Jones 1970).

According to Lewis (1954), *Hexaglottis* is most closely related to *Homeria* though she considered it in some respects less specialised, e.g. the style branches are slender in *Hexaglottis* but large and sub-petaloid in some of Homeria (fig. 5). The similarity of the karyotypes of species of *Homeria* to *Hexaglottis flexuosa* tends to confirm Lewis' opinion. *H. virgata* is a more specialised species of *Hexaglottis* for it is the only one possessing a perianth tube and it also has sessile flowers, completely lacking the short pedicels found in other species. Thus it is unlikely that the most specialised species of *Hexaglottis* should have a primitive karyotype. This is more likely a case of aneuploid reduction accompanied by a redistribution of chromosome material which has resulted in the unusual karyotype of *H. virgata*. This hypothesis could possibly be tested if this species could be crossed with another *Hexaglottis*. This would be a little difficult for the flowers last for only a few hours and wilt rapidly, but the cross could be performed if the species were cultivated together under laboratory conditions.

The evolution and significance of the style in *Hexaglottis* is problematic. It is this character which distinguishes *Hexaglottis* from *Homeria*. The three style branches are opposite the stamens but are forked almost to the base so that they extend on either side of the anther (fig. I, J). Thus there appear to be six style branches, two between each anther. In *Homeria* the style branches are only slightly forked above each of the three stigmas but *Hexaglottis* has a stigmatic area at the tip of each style branch.

If, as already discussed, the almost petaloid style of Homeria is reduced from that of *Moraea*, *Hexaglottis* can be interpreted as having a further reduced style where the petaloid nature has been lost completely. This interpretation implies that *Hexaglottis* is not more primitive than *Homeria*, as Lewis suggested, but rather derived from it. Unfortunately, there do not appear to be any other features in the two genera which differ sufficiently to throw light on the relationship between them.

g. The genus *Ferraria*

$2n = 20, 60.$

Ferraria is a comparatively small genus of perhaps twelve species. It is found from tropical Africa to the Cape Province where most species occur. These species were studied here, all from the south western Cape Province (Table 7). *F. longa* and *F. framesii* have a diploid number of 20, while *F. undulata* was found to be hexaploid with a somatic number of 60. Three geographically separate populations of this species were examined and all exhibited the same level of polyploidy.

There has been no previous report on the cytology of this genus. It appears from the present study that the basic number for the genus is 10. The chromosomes are long but the karyotype is distinctive in having a large number of comparatively short chromosomes (fig. 15).

Ferraria belongs to the *Irideae* and has the elaborate style with stamens opposite the branches, found in many genera of the group. It is unusual in having a feathery dissected petaloid apex of the style above the stigma. The perianth segments are subequal and spreading with the distal portions reflexed downwards and the margins of the segments are crisped. Most species are unpleasantly scented, and have rather dull markings characteristically in the form of spots. The flower thus appears to be very specialised and it is believed to be modified for pollination by flies.

The vegetative parts of the plant are less modified; the rootstock is a type of corm; the leaves are equitant, and the plant much ramified. The corm is peculiar for it has very fine tunics which soon disintegrate. Because these fine tunics were often overlooked the rootstock was often regarded as a tuber. The corms are persistent and plants often have the corms of several past seasons attached in a line to the growing portion. The corm itself is of the single internode type found in other African *Irideae* but it is probably less specialised than these in being long lived and having rather poorly developed tunics.

Ferraria has in the past been regarded as more closely allied to the South American genera of the *Irideae*, e.g. *Tigridia*, than to any South African group. *Tigridia* has a flower superficially resembling that of *Ferraria* but the style and stigma are not petaloid or dissected and the rootstock is a bulb, not a corm. Cytologically the two genera differ, for although the chromosomes are relatively large, the diploid number in *Tigridia* and in closely allied genera has been shown to be consistently 28 (Molseed 1970). The resemblance between these two genera may thus be entirely fortuitous.

The present author prefers to regard *Ferraria* as a derivative of the South African *Irideae* which diverged early from the line leading to *Moraea* but after the single internode of the group corm had been evolved.

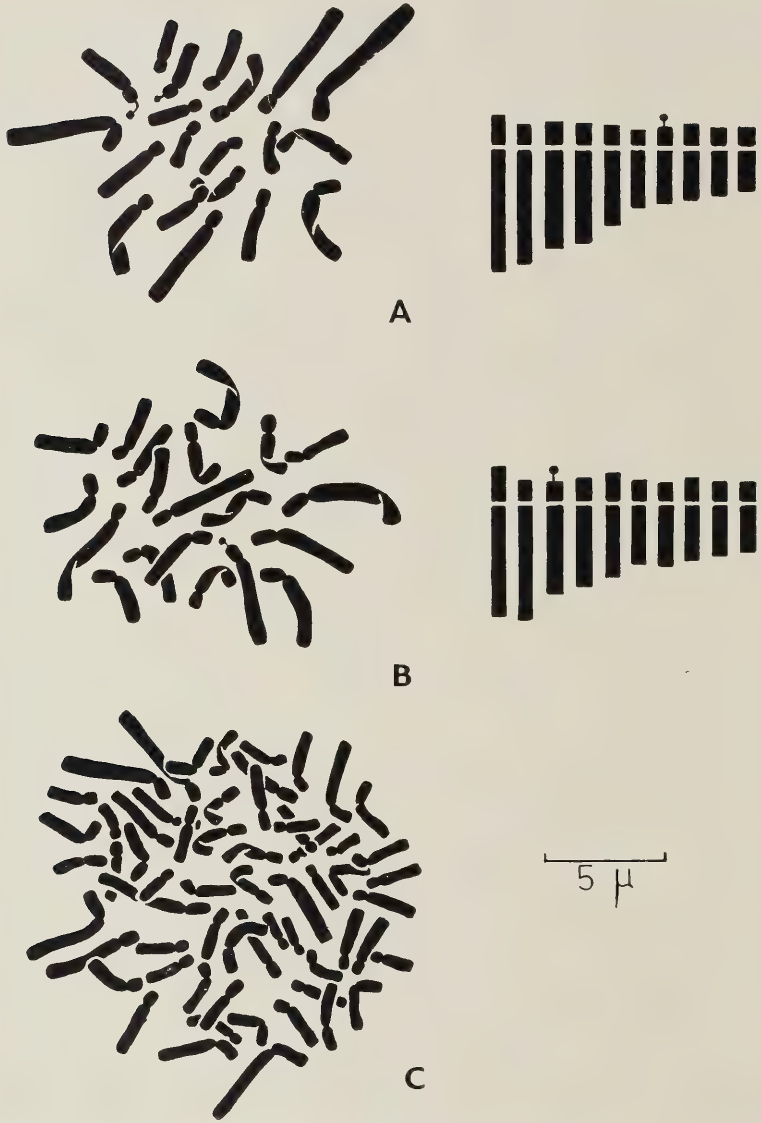


FIG. 15.
Karyotypes and idiograms of *Ferraria*. A. *Ferraria longa;* B. *F. cf. framesii;* C. *F. undulata.*

h. Conclusions

The subdivisions of the tribe *Irideae*

It is proposed to recognise three subtribes in the southern African members of the Irideae. *Dietes*, *Moraea* and *Gynandriris* together with *Iris* appear to comprise a single natural unit, the subtribe *Iridineae*. Although some variation does occur in several vegetative characters, the petaloid nature of the style branches and the unequal perianth segments are common to all representatives. *Homeria*, *Hexaglottis* and *Galaxia* probably form a second natural group for which the name *Homeriineae* is suggested. In this group the style is not petaloid and the perianth segments are subequal and spreading. *Ferraria*, with its equitant leaves and persistent corm with membranous tunics in contrast to the usually bifacial leaves and short-lived corm covered by fibrous tunics, does not fit in either of the above groups and must be placed in a third subtribe *Ferrariineae*. Whether this last genus is really allied to the new world genera as is often suggested, remains unknown at present and these must be examined more critically both morphologically and cytologically.

4.4. Tribe 3. IXIEAE.

Members of this tribe are mainly African in distribution. It comprises about thirty-three genera only three of which extend into Europe and Asia. Generally the group is distinguished by a cormous rootstock, equitant leaves, though these are often modified, and a spicate inflorescence of non-fugaceous flowers. Considerable specialisation of various structures has occurred in some genera, resulting in reduced plants such as *Crocus* which appear an exception to the above description.

CYTOLOGY, POSSIBLE PHYLOGENY AND CLASSIFICATION INTO SUBTRIBES

a. Subtribe ***Watsoniineae***

Watsonia, Pillansia, Thereianthus & Micranthus

This group is distinguished by the tough fibrous corm tunics, very fibrous, ensiform leaves and, with the exception of *Pillansia*, a spicate inflorescence with the flowers arranged distichously. The flowers have a well-developed perianth tube and forked style branches.

WATSONIA

$2n = 18, 27.$

Watsonia is a large genus of typically montane species occurring in southern Africa and Madagascar. When found in low lying areas the plants are associated with damp conditions. The species vary in size, many being the largest plants in the tribe, and reaching to about 1,5 m. The flowers are large and brightly coloured, the seeds are distinct from the other genera in this group in being winged and the leaves always fairly broad and sword shaped.

Table 8

Chromosome numbers in *Watsonia, Pillansia, Thereianthus* and *Micranthus.*

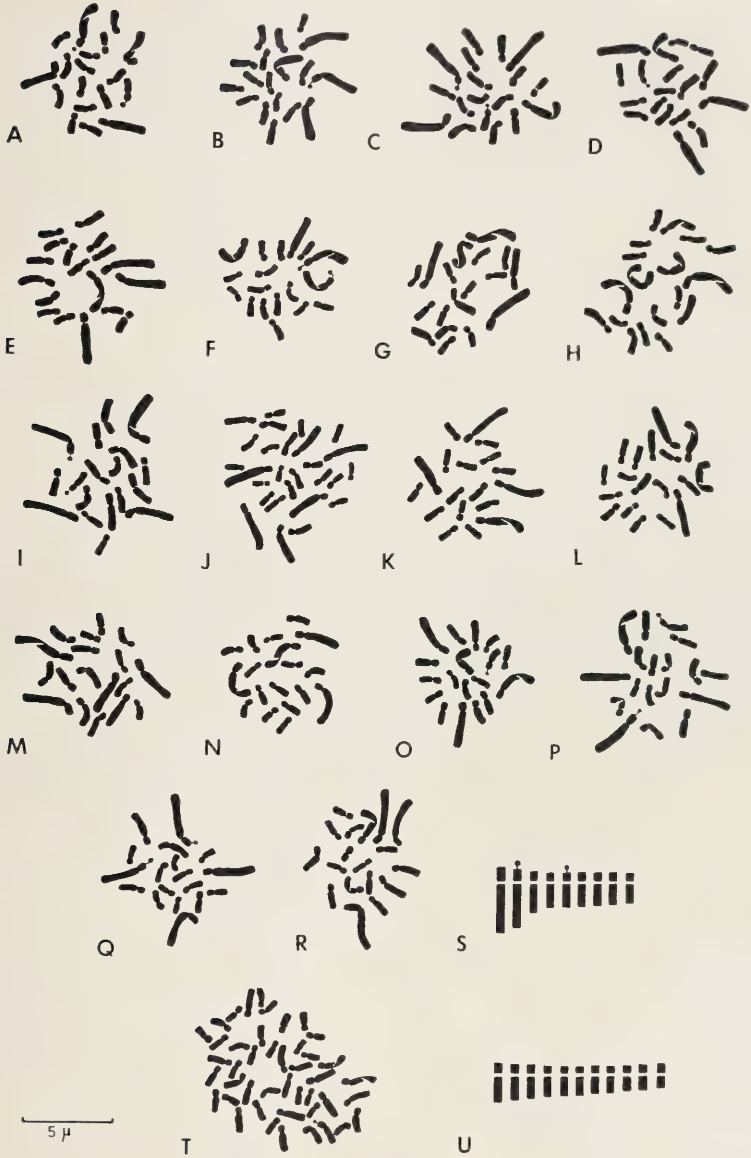
Species	Diploid No.	Collection Data or Reference
WATSONIA Miller		
W. brevifolia Ker	18	Napier, C.P. *Goldblatt 337*
W. ardernei Sanders	18	Kirstenbosch (ex hort) *Goldblatt 57* (J)
	16 + 2	(Riley 1962)
W. pyramidata (Andr.) Stapf. .	18	Stettyns Kloof, C.P. *Goldblatt 468*
W. beatricis Mathews & L. Bol.	18	Kirstenbosch, C.P. (ex hort) *Goldblatt 58* (J)
W. aletroides Ker	18	Caledon, C.P. *Goldblatt 38* (J)
W. fulgens (Andr.) L. Bol. . .	18	Skurweberg, Ceres, C.P. *Goldblatt 482*
W. humilis Miller	18	Table Mountain, C.P. *Goldblatt 405*
W. meriana Miller	18	Oudekraal, C.P. *Goldblatt 140* (J)
W. tabularis Mathews & L. Bol.	18	Cape Point Reserve, C.P. *Goldblatt 155* (J)
W. bulbillifera Mathews & L. Bol.	27	Kirstenbosch, C.P. (ex hort) *Goldblatt 53* (J)
W. vivipara Mathews & L. Bol. .	18	Ceres, C.P. *Goldblatt 477*
W. angusta Ker.	18	Stettyns Kloof, C.P. *Goldblatt 476*
W. transvaalensis Bak. . . .	18	Haenertsburg, Tvl. *Goldblatt 56* (J)
W. alpina Lewis	18	Graskop, Tvl. *Goldblatt 522* (J)
W. latifolia Oberm	18	Wakkerstroom, Tvl. *Goldblatt 76* (J)
W. galpinii L. Bol.	18	Eastern C.P. *Goldblatt 84* (J)
W. stenosiphon L. Bol. . . .	18	Quoin Point, C.P. *Goldblatt 479*
W. marginata (L.f.) Ker. . . .	18	Kirstenbosch, C.P. (ex hort) *Goldblatt 488*
W. fourcadei Mathews & L. Bol.	18	(Riley 1962)
W. sp. (as W. iridifolia) . . .	18	(Sharma & Talukdar 1960)
	18	(Nakajima fide Darlington & Wylie 1955)
W. hort. var.	16	(Brittingham 1934)
PILLANSIA L. Bol.		
P. templemanii (Bak) L. Bol. .	44	Rooi Els, C.P. *Goldblatt 471*
THEREIANTHUS Lewis		
T. bracteolatus (Lam) Lewis . .	20	Houw Hoek Pass, C.P. *Goldblatt 68* (J)
T. lapeirousioides (Bak.) Lewis .	20	Bains Kloof, C.P. *Goldblatt 190*
MICRANTHUS Pers. ex. Eckl.		
M. plantagineus (Pers) Eckl. . .	20	Elgin, C.P. *Goldblatt 69* (J)
M. tubulosus (Burm.) N. E. Br. .	20	Kirstenbosch, C.P. (Ex hort) *Goldblatt 489*
M. junceus (Bak.) N. E. Br. . .	20	Caledon, C.P. *Goldblatt 395*

All localities given are in South Africa unless otherwise stated. Provinces are abbreviated as follows: Cape Province—C.P., Transvaal—Tvl. Specimens are housed in the Bolus Herbarium unless stated to the contrary.

Eighteen of the approximately seventy recognised species were studied, (Table 8) and all except one have a diploid number of 18 comparatively small chromosomes. The karyotype is very characteristic, consisting of 2 pairs of long chromosomes, measuring between 2 and 4μ, a pair of medium length of

Fig. 16.

Karyotypes and idiograms of *Watsonia* and *Pillansia*. A. *Watsonia brevifolia;* B. *W. ardernei;* C. *W. pyramidata;* D. *W. beatricis;* E. *W. aletroides;* F. *W. fulgens;* G. *W. humilis;* H. *W. meriana;* I. *W. tabularis;* J. *bulbillifera;* K. *W. vivipara;* L. *W. angusta;* M. *W. transvaalensis;* N. *W. alpina;* O. *W. latifolia;* P. *W. galpinii;* Q. *W. stenosiphon;* R. *W. marginata;* S. Idiogram of *Watsonia;* T. *Pillansia templemanii;* U. Idiogram of *Pillansia.*


A
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about $2,5\mu$ and the remaining 6 pairs of short chromosomes of about $1,5\mu$ long (fig. 16: A—S). The exception is *W. bulbillifera* which has 27 somatic chromosomes. This species is clearly triploid and as would be expected has 6 long, 3 medium and 18 short chromosomes.

The chromosomes are acrocentric and there appear to be satellites on two pairs of chromosomes. Although all the satellites are seldom seen, several metaphase plates exhibit a satellite on one of the long and one of the short chromosomes. This characteristic is believed to be constant though difficult to see and is represented in the idiogram of *W. pyramidata* shown here as representative of the genus.

Prior to this study, only four species of *Watsonia* had been described cytologically. Brittingham (1934) found a diploid number of 16 in an unidentified horticultural variety. Darlington & Wylie reported that Nakajima found a diploid number of 18 in *W. iridfolia* (a name used for many horticultural forms, but probably close to *W. meriana*). Sharma and Talukdar (1960) also found $2n = 18$ for a form they referred to *W. iridifolia*. Riley found $2n = 18$ in *W. fourcadei*, but in *W. ardernei* $2n = 16$ plus two supernumaries. Present investigation of *W. ardernei* revealed that it does not differ from the other species of *Watsonia* but has 18 somatic chromosomes. Thus the supernumaries described by Riley for this species were probably a pair of small somatic chromosomes. Brittingham, who also found a diploid number of 16 may have been mistaken in his interpretation of the karyotype. His illustration shows 6 long chromosomes, 2 of which have marked medium constrictions, and these are probably really 2 small chromosomes lying very close together. If this interpretation is correct, Brittingham's work is in accord with the other chromosome studies in *Watsonia*.

Sharma and Talukdar described the karyotype of the species they studied as consisting of 4 long, 2 medium and 12 short chromosomes. Essentially the same results were obtained in the eighteen species studied by the present author. As altogether twenty of the seventy species of *Watsonia* have now been cytologically studied, it can be said with confidence that the basic number is 9 and the karyotype consists of 2 long pairs of chromosomes, one bearing a satellite, 1 medium pair and 6 short pairs, one of these also bearing a satellite.

The observation that *W. bulbillifera* has 27 chromosomes indicates that this species is triploid. An examination of pollen mother cells undergoing meiosis revealed the reduction division was totally abnormal and many trivalents and univalents occur. Though pollen is formed it is abnormal and there is an extraordinary variation in pollen grain size. The suggestion that this is a sterile triploid species is substantiated by the fact that it does not reproduce sexually but by means of cormlets which are produced in great numbers from all the nodes on the penduncle after flowering is over.

W. bulbillifera is closely related to *W. vivipara* which also produces large numbers of bulbils. In this case, however, the bulbils are produced while the plant is flowering. This latter species does reproduce sexually and produces viable seed. It has a wide distribution, occurring in the Warm Bokkeveld and the Montagu Karoo, while *W. bulbillifera* is restricted to the Cape Flats and Peninsula. *W. vivipara* is slightly smaller than *W. bulbillifera* in both flower size, height and leaf width but the differences are only quantitative, and to be expected between diploid and polyploid. It is likely that *W. bulbillifera* is only a race differing cytologically from its parent species, *W. vivipara*. The possibility of allopolyploidy cannot, however, be excluded, which would imply a hybrid origin with *W. vivipara* as one of the parents.

PILLANSIA

$2n = 44$.

Pillansia is a monotypic genus and is restricted to the coastal portion of the Caledon area of the western Cape. Vegetatively, the plant resembles *Watsonia*, but the inflorescence is branched and panicle-like and the corms are persistent. *Pillansia templemanii* has a diploid number of 44. The chromosomes are all acrocentric and small (fig. 16: T), ranging from 1 to 2μ in length. Careful examination reveals that there are 4 pairs of somewhat longer chromosomes which may be described as medium in length. As this species is believed to be a polyploid (as will be discussed later) the idiogram is shown comprising only eleven chromosomes (fig. 16: U).

This is the first chromosome count for this species. The somatic number of 44 is unusually high and indicates the possibility of polyploidy. To exclude the possibility of an isolated polyploid population having been studied, a geographically separate population was also examined. Here also the somatic number was found to be 44. A study of meiosis in pollen mother cells revealed 22 bivalents and meiosis appeared to be quite normal, thus indicating autopolyploidy as unlikely, although recent work has shown that bivalents only, may occur in known autopolyploids.

Pillansia templemanii is an unusual species which has a very limited distribution. It was believed by Lewis (1954) to be the ancestor of *Watsonia* and its allies because it has many of the watsonioid characteristics, e.g. the tough corm tunics, broad fibrous leaves and bifid stigmas. Its more primitive characteristics are its regular flowers, short perianth tube and branching paniculate inflorescence. It is thus believed to be a relict polyploid belonging to the group of plants which gave rise to the more specialised *Watsonia* and allies.

MICRANTHUS

$2n = 20$.

Micranthus is a small genus found in the south western Cape Province. The plants are small and flower in early summer. The resemblance to *Watsonia* is strong, but the flowers are very small and the leaves narrow to terete.

The three species in the genus were all found to have a diploid number of 20 (Table 8). All have a similar karyotype which consists of a single pair of long chromosomes of about 3μ in length, a pair of medium chromosomes measuring 2μ and 8 pairs of small chromosomes measuring less than $1{,}5\mu$ (fig. 17: A, B, C). The chromosomes are acrocentric and the long pair bears a satellite. The idiogram shown here is based on all three karyotypes (fig. 17: D). The chromosome counts are new records for the genus which clearly has a basic number of 10.

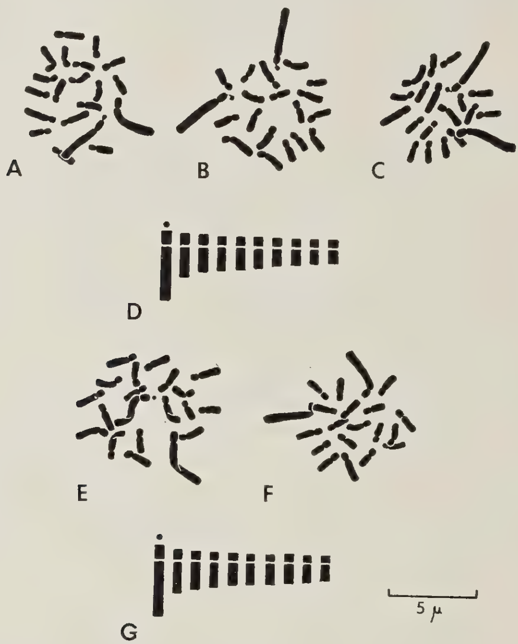

FIG. 17.
Karyotypes of *Micranthus* and *Thereianthus*. A. *Micranthus plantagineus;* B. *M. tubulosus;* C. *M. junceus;* D. Idiogram of *Micranthus;* E. *Thereianthus bracteolatus;* F. *T. lapeirousioides;* G. Idiogram of *Thereianthus*.

THEREIANTHUS

$2n = 20.$

Thereianthus is a small genus closely allied to *Watsonia*. The plants are small, usually purple flowered and bloom in summer. The narrow to terete, mucronate leaves are like those of *Micranthus*.

Two of the eight species, *Thereianthus bracteolaris* and *T. lapeirousioides* were studied by the present author. In both the diploid number is 20 (fig. 17: E, F) and the karyotypes similar to those of *Micranthus*. Again a general idiogram is illustrated, based on both species studied (fig. 17: G). The resemblance to *Micranthus* is quite unmistakable.

The two counts in this work are new records for the genus. *Thereianthus* was established by Lewis (1941) as a segregate of *Watsonia* and consisted of the smaller flowered summer blooming species then included in *Watsonia*. The difference in the karyotype is added confirmation of the validity of Lewis' treatment.

Although only two of the six species in the genus were studied, it is assumed that these are representative and that the basic number for the genus is 10. A comparison of the idiograms of *Micranthus* and *Thereianthus* shows the remarkable similarity of their karyotypes. It is clear that although *Thereianthus* was comparatively recently recognised as a segregate of *Watsonia* it is in fact more closely related to *Micranthus*.

Although the karyotypes are so similar and the two genera have several morphological features in common, the differences in the inflorescence and flower structure indicate that they should continue to be considered separate entities. While their corms are very similar and the mucronate leaves of both are unique in the family, their flowers and inflorescences are characteristic.

Thereianthus has a few quite large, either actinomorphic or subzygomorphic, flowers with a straight perianth tube, while *Micranthus* has many small zygomorphic flowers with a curved perianth tube.

Evolution of *Watsonia* and its allies

Pillansia is believed to be the ancestor of *Watsonia* and its allies though as mentioned, *P. templemanii* appears to be a relict polyploid. If this assumption is correct, the evolution of the group has been accompanied by a decrease in the chromosome number. The reduction in number has presumably taken place by unequal translocation in two chromosomes and the loss of the centromere in one of them by the method postulated by Darlington (1937) and later discovered in several organisms. This step would thus result in a karyotype like that found today in *Thereianthus* and *Micranthus* where there are a pair of long chromosomes. Further aneuploid reduction would result in the *Watsonia* karyotype with two pairs of long chromosomes.

The aneuploid reduction has been accompanied by a degree of morphological specialisation. The corm is short-lived in *Watsonia*, *Micranthus* and *Thereianthus* in contrast to the persistent type found in *Pillansia*. The evolution of the specialised genera from *Pillansia* is unlikely to have been direct, for the zygomorphic many-flowered *Micranthus* could not have given rise to the actinomorphic

species of *Watsonia*. It is more likely that *Watsonia* represents one line and *Micranthus* another, both leading from *Pillansia* through *Thereianthus* where species with actinomorphic flowers predominate.

The bifid stigmas in this group were once regarded as an important taxonomic character and were the reason for *Lapeirousia* and *Freesia* being included in the tribe *Watsonieae* of Pax. The cytological data does not necessarily support this treatment, for although *Freesia* has 22 somatic chromosomes and several *Lapeirousia* species have a diploid number of 20, the karyotypes are unlike those found in *Watsonia* and its allies where the same numbers occur. Bifid stigmas also occur in species of *Crocus*; they are a characteristic feature of *Romulea* and are found in some species of *Crocosmia* such as *C. aurea* and in *Oenostachys dichroa* (Bullock 1930). *Romulea* and *Crocus* do not appear to be allied to the *Watsonia* group and neither does *Crocosmia*. These are more likely examples of parallel evolution, and it seems quite possible that bifid stigmas evolved independently in *Lapeirousia* and *Freesia* so that they should not be used alone as evidence of phylogenetic relationship.

In her classification, Lewis (1954) placed *Pillansia* in its own subtribe *Pillansiineae*, and *Watsonia*, *Thereianthus* and *Micranthus* with *Freesia* and *Lapeirousia* in the *Watsoniineae*. This treatment, in which Lewis recognises the relationship between *Watsonia* and *Pillansia*, is not followed for it is proposed that *Pillansia* be included in the *Watsoniineae*. *Freesia* and *Lapeirousia* are excluded from the group as it is believed that they are not very closely allied to *Watsonia*.

b. Subtribes ***Lapeirousiineae and Freesiineae***
Lapeirousia, *Anomatheca* & *Freesia*

This group comprises two discordant elements, *Lapeirousia* proper, i.e. the subgenera *Sophronia* and *Lapeirousia* (*Ovieda* of Baker) and *Freesia* and *Anomatheca*, previously the subgenus *Anomatheca* of *Lapeirousia*. Both groups are small herbaceous geophytes occurring throughout southern Africa. They differ consistently in several significant features which will be discussed in detail below. The three genera are dealt with together here, because they have, in the past, been regarded as closely allied, the main reason for this being the nature of the style branches which, in both genera, are deeply forked.

LAPEIROUSIA

(including only subgenera *Lapeirousia* (*Ovieda*) and *Sophronia*)

2n = 20, ?18.

The genus, as circumscribed in this paper, i.e. excluding subgenus *Anomatheca*, comprises plants having a bell-shaped corm with a woody, entire tunic, a single basal leaf and large herbaceous floral bracts. The flowers, though very varied, are usually long tubed and have forked style branches.

There are about thirty species in the two subgenera. Eight of the approximately twenty species which occur in the winter rainfall area of the Cape Province were examined cytologically. The diploid number was clearly 20 in some species (Table 9), while in others it could not be established with certainty, 18, 19 or occasionally 20 somatic chromosomes being seen in different cells. It seems likely that these species also have 2n = 20 and that owing to the very small size of the chromosomes, one or two were sometimes overlooked, possibly being masked by others lying over them. The likelihood that the diploid number is 18 rather than 20 has been rejected, though this cannot be established for certain with present methods of examination and it remains possible that the last chromosome pair are simply large satellites.

TABLE 9
Chromosome numbers in *Lapeirousia, Anomatheca* and *Freesia.*

Species	Diploid No.	Collection Data or Reference
LAPEIROUSIA		
Subgenus 1. Sophronia		
L. oreogena Schlechter ex Goldblatt ined.	ca 18	Nieuwoudtville, C.P. *Goldblatt 245*
Subgenus Lapeirousia (=Ovieda Baker)		
L. corymbosa (L.) Ker	20	Tulbagh, C.P. *Goldblatt 203*
L. micrantha Meyer ex Klatt	20	Giftberg, C.P. *Goldblatt 374*
L. fastigiata (Lam.) Ker	20	Paarl flats, C.P. *Goldblatt 456*
L. fissifolia (Jacq.) Ker	ca 20	Montagu, C.P. *Goldblatt 428*
L. jacquinii N. E. Br.	ca 20	Piketberg, C.P. *Goldblatt 232*
L. anceps (L.f.) Ker	20	
L. divaricata Bak.	ca 20	
ANOMATHECA		
A. laxa (Thunb.) Goldblatt	22	Inhaca Island, Mozambique. *Goldblatt 1* (J)
(as Lapeirousia cruenta)	16	(Brittingham 1934)
(as L. cruenta)	22 (publ. in error as 20.)	(Dyer 1963)
A. grandiflora Bak.	22	Johannesburg, Tvl. *Goldblatt, 8, 9* (J)
A. verrucosa (Vog.) Goldblatt (=A. juncea)	22	near Avontuur, C.P. *Goldblatt 451.*
A. fistulosa (Spreng. ex. Klatt) Goldblatt	22	Camps Bay, C.P. *Goldblatt 517*
A. viridis (Lindl.) Goldblatt	22	Saldanha district, C.P. *Goldblatt 252*
FREESIA Klatt		
F. elimensis L. Bol.	22	Bredasdorp, C.P. *Goldblatt 379*
F. muirii N. E. Br.	22	Southern C.P. *Goldblatt 145* (J) (ex hort)
F. c.f speciosa L. Bol. (non flowering material)	22	Ladismith, C.P. *Goldblatt 491*
F. refracta (Jacq.) Klatt	22	Worcester, C.P. *Goldblatt 143* (J)
	22	(Taylor 1926)
F. cultivars	22, 33	(Brittingham 1934)

All localities given are in South Africa unless otherwise stated. Provinces are abbreviated as follows: Cape Province—C.P.; Transvaal—Tvl. Unless stated to the contrary, material is housed at the Bolus Herbarium, Cape Town.


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In one species, *L. oreogena* (subgenus *Sophronia*) only 18 chromosomes could be detected, but whether this really represents a difference between it and the other species examined, all of which belong to subgenus *Lapeirousia*, is uncertain because of difficulties in counting the smallest chromosomes.

The karyotype of *Lapeirousia* is remarkable in that it consists of a single pair of very large chromosomes and the remainder (whether eight or nine pairs) are all very small. One or sometimes two satellites are found on short chromosomes and are assumed to be a constant feature of the karyotype. The idiogram shown here (fig. 18: I) consisting of 10 chromosomes, is based on the karyotype of *L. corymbosa* and is assumed to be representative of the genus.

The karyotype is peculiarly asymmetrical in having the single pair of very large chromosomes. This pair of chromosomes are amongst the largest in the tribe *Ixieae* and more like those found in the *Irideae*. There are approximately twenty species in these two subgenera in the winter rainfall region of southern Africa and about ten more in the summer rainfall region of south and tropical Africa. Perhaps when more species are examined cytologically, particularly those in the summer rainfall region, none of which were available, intermediate karyotypes may be found, leading to the very asymmetrical one occurring in those winter rainfall specimens studied.

ANOMATHECA

$2n = 22.$

There are perhaps six or seven species in the subgenus, occurring in both summer and winter rainfall areas of southern Africa. *Anomatheca* is distinguished by its conical corms with reticulate fibres, several basal leaves and short rather membranous floral bracts. Five species were examined by the present author (Table 9). One species, *A. fistulosa* was previously referred to *Lapeirousia* but due to its karyotype and morphology it is treated as an *Anomatheca* here. In all five species a diploid number of 22 was obtained. The chromosomes are mostly acrocentric but some of the smaller ones are sub-metacentric. The chromosomes range in length from approximately 1,5 to 3μ. As in *Freesia*, in which the karyotype is very similar, there are two or three pairs of longer chromosomes (fig. 18: J—O).

The only species of *Lapeirousia* which has previously been cytologically examined, *A. laxa* is a member of the subgenus *Anomatheca*. Brittingham (1934) reported a diploid number of 16 for this species, known to him as *L. cruenta*.

FIG. 18.

Karyotypes and idiograms of *Lapeirousia*, *Anomatheca* and *Freesia*. A. *Lapeirousia oreogena;* B. *L. corymbosa;* C. *L. micrantha;* D. *L. fastigiata;* E. *L. fissifolia;* F. *L. jacquinii;* G. *L. anceps (fabricii);* H. *L. divaricata;* I. Idiogram of *Lapeirousia;* J. *Anomatheca laxa;* K. *A. grandiflora;* L. *A. juncea;* M. *A. fistulosa;* N. *A. viridis;* O. Idiogram of *Anomatheca;* P. *Freesia refracta;* Q. *F. muirii;* R. *F. elimensis;* S. *F. cf. speciosa;* T. Idiogram of *Freesia*.

Dyer (1963) reported a diploid number of 20 for the same species (also as *L. cruenta*). This report of 2n = 20 is a typographical error for Dyer (private communication) has stated that the diploid number is 22. Dyer (private communication) also found that the karyotype consisted of small chromosomes with one pair of satellite chromosomes which thus appeared rather larger.

Brittingham's report of 2n = 16 for *A. laxa* seems in light of the present author's confirmation of Dyer's report, to be erroneous and it appears that Brittingham may have misinterpreted the karyotype of this plant.

FREESIA

2n = 22.

Freesia is a small genus comprising at present about twenty species. It is in need of revision for there are without doubt fewer species than are recognised today. It is similar in most respects to *Anomatheca*, differing mainly in having a horizontal, inflexed inflorescence, and scented flowers with a long bottle-shaped perianth tube. Four species were examined by the present author and in all a diploid number of 22 was obtained. The chromosomes are acrocentric and range in size from 1,5 to 3μ. Although the chromosome length forms a continuous series, two or three pairs of larger chromosomes can be distinguished and satellites appear to be located on one of these pairs (fig. 18: P—T).

The karyotype of *Freesia* was first described by Taylor (1926) who found a diploid number of 22 in a horticultural form of *F. refracta*. Brittingham (1934) also examined horticultural stock and found diploid numbers of 22 in several cultivars and 44 in another. The present study confirms that the basic number for the genus is 11 but the counts for the four species studied here are new records for wild species.

The status of *Anomatheca*.

Anomatheca was a genus established by Ker (1805) for *A. verrucosa* (as *A. juncea*) previously regarded as a *Gladiolus*. The main reasons for the creation of the genus were the bifid stigmas, reticulate corm tunics and the peculiar rough surfaced capsule, all features being quite unlike those found in *Gladiolus*. *Anomatheca* was recognised by Baker (1876) but later he reduced it to the rank of a subgenus in *Lapeirousia* (Baker 1892). This treatment was followed in *Flora Capensis* and has subsequently been maintained.

Lewis (1954) considered that *Lapeirousia* sensu Baker was an unnatural group and suggested that *Anomatheca* was in fact more closely related to *Freesia* than to the rest of *Lapeirousia*. This opinion is supported by the present author on cytological and morphological grounds and *Anomatheca* is reinstated here as a valid genus. It is very closely related to *Freesia* and if there is to be consistancy in the treatment of genera the two should perhaps be merged.

Excluding *Anomatheca*, *Lapeirousia* consists of plants which have the following characteristics: a distinctive flat based corm with hard entire tunics; one or two basal leaves; an inflorescence frequently much ramified; actinomorphic or zygomorphic flowers with bifid stigmas and a capsule with a smooth, membranous surface. *Anomatheca* has in contrast a round based corm with reticulate tunics, several basal leaves, only one or two branches on the inflorescence and zygomorphic flowers with a long perianth tube and a distinctive rough surface capsule. *Freesia* has all these features which are characteristic of *Anomatheca* and the only difference between the two is in the form of the perianth tube. In *Freesia* the tube is elongate-infundibuliform and in *Anomatheca* varies as it is either turbinate or curved with a wide throat. These differences are of a minor nature and do not seem to constitute a reason for separating the genera.

The cytological evidence supports the contention that *Freesia* and *Anomatheca* are closely related as they have a similar karyotype with a diploid number of 22. The remainder of the species of *Lapeirousia* has a quite different and distinctive karyotype and with the suggested diploid number of 20. The intergeneric crosses attempted by the author between *Freesia* and *Anomatheca* did not succeed. Further crosses should be attempted, especially between other species in the two genera. The failure of the crosses does, however, constitute a piece of evidence against the contention of a very close relationship between *Freesia* and *Anomatheca*, because most species in genera in the *Ixieae* are interfertile. If more crosses are tried and fail, then the two genera should perhaps be maintained as separate entities. If, however, these succeed the possibility of merging *Freesia* and *Anomatheca* should be seriously considered.

The position of *Lapeirousia fistulosa*

Lapeirousia fistulosa is a fairly well-known plant which has long been considered as belonging to the subgenus *Lapeirousia*. The discovery that its karyotype was like that of *Anomatheca* prompted a close examination of the plant. It is rather small and reduced and often bears a single flower. When it has more than one flower these appear pedicellate but the flowers should rather be considered as solitary branches. This accords with the occurrence of sessile flowers in the whole of the tribe *Ixieae*. The corm of this species is small and spherical but the tunics are clearly of reticulate fibres and not woody as in *Lapeirousia* proper.

This species has only two well-developed leaves and these are broad and soft in texture and quite unlike those found in most species of *Lapeirousia* where only one rigid and ribbed leaf occurs. The bracts are fairly small and rather dry like those found in *Anomatheca*. One feature which does not agree with this subgenus is the capsule. This in *Anomatheca* is typically broader than high, has a rather firm, rough papillate outer surface and contains large ovoid

seeds. *Lapeirousia fistulosa* has a rather elongated smooth walled capsule containing small angled seeds. This latter type of fruit is found in *Lapeirousia* (sensu stricto) and also in many other genera such as *Hesperantha* and *Tritonia*. Both morphological and cytological evidence are strongly in favour of the transfer of this species to *Anomatheca*, which must itself be slightly expanded in concept to include this somewhat reduced plant.

The relationship between *Lapeirousia* and *Anomatheca* and *Freesia*

The relationship between *Anomatheca* and *Freesia* on the one hand and *Lapeirousia* (sensu stricto) on the other, is not, in the present author's opinion, a close one. The only feature in common is the bifid stigma which, as discussed under *Watsonia*, is believed to have evolved independently at least twice in the family, and is probably not as important a feature as was previously believed. The type of corm and the nature of the corm tunics are a far more reliable taxonomic character at generic level. In this feature, *Lapeirousia* is different from most of the other *Ixieae*, having a bell-shaped corm with entire and usually hard tunics. Other groups which have the most similar type of corm are *Hesperantha* and its allies, and *Romulea*. In these genera the corm has hard, entire tunics but with a smooth surface in contrast to *Lapeirousia* in which the surface is rather rough. In *Hesperantha*, its allies and *Romulea* the corm usually consists of one or only a few internodes and the roots emerge from only one side of the base of the corm which is extended to form a ridge so that these corms can be described as asymmetric, though some species of Romulea have a circular basal ridge. In *Lapeirousia* the corm also consists of very few internodes, but the roots emerge from all sides of the base of the corm.

Thus, a relationship between *Lapeirousia* and *Hesperantha* and its allies as suggested by the similarity of their corms is not as close as appears at first. *Lapeirousia* has frequently been grouped with *Watsonia* owing to the bifid nature of the stigmas in both of them. There are, however, no other indications of close relationship.

The type of corm with several internodes in *Freesia* and *Anomatheca* occurs in most genera of the *Ixieae* but the reticulate tunics are less common. *Sparaxis*, *Ixia* and *Tritonia* have a corm most like that of *Anomatheca* and this may indicate some relationship between them. Karyologically *Freesia* and *Anomatheca* appear to be allied to *Tritonia* ($2n = 22$) and less to *Ixia* and *Sparaxis* ($2n = 20$). There is, however, no strong evidence to indicate the affinity between *Freesia* and *Anomatheca* on the one hand and any particular group in the *Ixieae* on the other. Accordingly the new subtribe *Freesiineae* is proposed for these two closely allied genera.

TABLE 10

Chromosome numbers in *Schizostylis, Hesperantha, Geissorhiza, Engysiphon* and *Melasphaerula*

Species	Diploid No.	Collection Data or Reference
SCHIZOSTYLIS Backh. & Harv.		
S. coccinea Backh. & Harv. . .	26	Haenertsburg, Tvl. *Goldblatt 12* (J)
HESPERANTHA Ker		
H. baurii Bak.	26	Graskop, Tvl. *Goldblatt 72* (J)
H. longituba (Klatt) Bak. . .	26	Graskop, Tvl. *Goldblatt 73* (J)
H. radiata (Jacq.) Ker. . . .	26	Touws River, C.P. *Goldblatt 146* (J)
H. angusta (Jacq.) Ker. . . .	26	Nieuwoudtville, C.P. *Goldblatt 229*
H. buhrii L. Bol.	26	Nieuwoudtville, C.P. *Goldblatt 243*
H. falcata (L.f.) Ker.	26	Cape Point Reserve, C.P. *Goldblatt 149* (J)
H. pilosa (L.f.) Ker.	26	Grasberg, near Nieuwoudtville, C.P. *Goldblatt 272*
H. puberula Schltr.	26	Nieuwoudtville, C.P. *Goldblatt 284*
H. flexuosa Klatt	26	Springbok, C.P. *Goldblatt 191*
H. vaginata (Sweet) Goldblatt .	26	Nieuwoudtville, C.P. *Goldblatt 259*
H. vaginata (Sweet) Goldblatt (=H. stanfordiae)	26	Nieuwoudtville, C.P. *Goldblatt 93* (J)
H. pauciflora (Bak.) Lewis . .	26	Nieuwoudtville, C.P. *Goldblatt 231*
H. spicata (Burm. f.) N. E. Br. .	26	Darling, C.P. *Goldblatt 416*
GEISSORHIZA Ker.		
G. splendidissima Diels . . .	26	Nieuwoudtville, C.P. *Goldblatt 347*
G. louisabolusii Foster . . .	26	Citrusdal, C.P. *Goldblatt 247*
G. imbricata (de la Roche) Ker .	26	(ex hort) *Goldblatt 165* (J)
G. aspera Goldblatt (=G. secunda)	52	Signal Hill, C.P. *Goldblatt 213*
	52	Simonstown, C.P. *Goldblatt 520*
(as G. secunda)	26	(Gwynn 1958)
G. heterostyla L. Bol. . . .	26	Voëlvlei, Sutherland, C.P. *Hall* (NBG)
G. inaequalis L. Bol.	52	Van Rhyns Pass, C.P.
		Nieuwoudtville, C.P. *Goldblatt 129* (J), *275*
G. leipoldtii Foster	26	Calvinia, C.P. *Goldblatt 135* (J)
G. bolusii Bak.	39	Bains Kloof; Grootkop, C.P. *Goldblatt 458, 515*
G. pusilla (Andr.) Klatt . . .	26	Signal Hill, C.P. *Goldblatt 196*
G. nana Klatt	26	Caledon, C.P. *Goldblatt 214*
G. ovata (Burm. f.) Asch. & Graeb.	26	Botrivier, C.P. *Goldblatt 217*
ENGYSIPHON Lewis		
E. exscapus (Thunb.) Lewis . .	26	Bains Kloof, C.P. *Goldblatt 483*
E. longifolius Lewis	26	Pakhuis Pass, Clanwilliam, C.P. *Goldblatt 122* (J)
E. brevitubus Lewis	26	Piketberg, C.P. *Goldblatt 204*
MELASPHAERULA Ker		
M. ramosa (L.) Ker N. E. Br. .	22	Nieuwoudtville, C.P. *Goldblatt 110* (J)

All localities given are in South Africa unless otherwise stated. Provinces are abbreviated as follows: Cape Province—C.P.; Transvaal—Tvl. Specimens are housed at the Bolus Herbarium unless stated to the contrary.

Lapeirousia, excluding *Anomatheca*, is a natural group although it does include a wide range of species with different habit and flower type. The flower ranges from actinomorphic short-tubed as found in *L. corymbosa*, to zygomorphic and long-tubed, as occurring in *L. arenicola* and in *L. fabricii*, where the perianth tube is curved and broad at the apex. As *Lapeirousia* does not appear to be closely allied to any other genus in the *Ixieae*, and has such a distinct type of corm, it is proposed that it be placed in its own subtribe *Lapeirousiineae*.

c. Subtribe ***Hesperanthineae***

Hesperantha, Schizostylis, Geissorhiza, Engysiphon, Melasphaerula

The representatives of this group of genera are all small herbaceous plants, generally having hard, woody corm tunics and fairly unspecialised, usually actinomorphic flowers. *Schizostylis* is an exception, the rootstock being rhizome-like.

HESPERANTHA

2n = 26.

Hesperantha is a fairly large genus occurring from central to southern Africa. The species are mostly small plants with small, regular, often scented flowers which open in the afternoon and evening. The genus can be distinguished by its bell-shaped corms with hard, woody corm tunics, and characteristic laterally projecting ridge and the style which divides at the mouth of the perianth tube into three long branches.

In all twelve species of *Hesperantha* studied, of a total of about fifty species, a diploid number of 26 was obtained (Table 10). The chromosomes are acrocentric and relatively uniform in size, ranging from 1,3 to 2,5μ in length (fig. 19). Although it is often possible to distinguish a group of larger chromosomes, the number of these is not constant in all species and the size of individual chromosomes does not form any constant feature of the karyotype. Satellites are occasionally seen on one or two of the smaller chromosomes.

The only previous report on the cytology of the genus, that of Fernandes and Neves (1961) for *H. falcata*, is confirmed in the present study. It is clear that the basic number in the genus is 13.

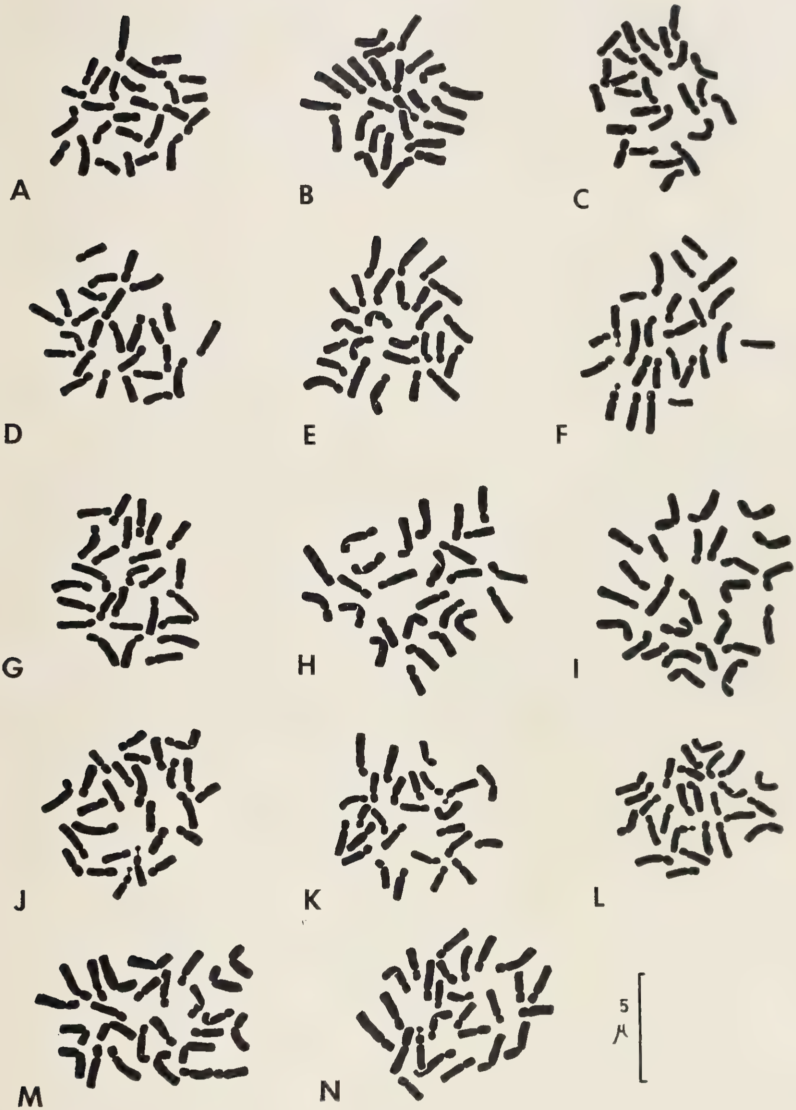
SCHIZOSTYLIS

2n = 26.

This is a small, possibly monotypic genus of streamside plants found in mountainous regions from central Africa to the eastern Cape Province. It is

Fig. 19.

Karyotypes of *Hesperantha* and *Schizostylis*. A. *Hesperantha baurii;* B. *H. longituba;* C. *H. radiata;* D. *H. angusta;* E. *H. buhrii;* F. *H. falcata;* G. *H. pilosa;* H. *H. puberula;* I. *H. flexuosa;* J. *H. vaginata;* K. *H. vaginata* (=*stanfordiae*); L. *H. pauciflora;* M. *H. spicata;* N. *Schizostylis coccinea.*


A
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5 μ

very similar to *Hesperantha*, having the same characteristic flowers and style branches. The only difference is the rootstock which in *Schizostylis* is a short thick rhizome-like structure.

One of the two doubtfully distinct species, *Schizostylis coccinea*, was examined cytologically for the first time. The diploid number was found to be 26 and the karyotype, which resembles that of species of *Hesperantha*, consists of acrocentric chromosomes which range from 1,2 to 2,5μ in length (fig. 19: N).

GEISSORHIZA

$2n = 26.$

Geissorhiza is a genus of about fifty species, occurring in the winter rainfall area of southern Africa. It is allied to *Hesperantha* which it closely resembles. The differences are that the style forks well beyond the mouth of the perianth tube and the style branches are shorter. The hard, overlapping corm tunics have a tendency to split vertically giving the corm a tiled appearance, a feature often useful in identification of non-flowering material.

Eleven of the approximately forty-five species in the genus were examined (Table 10). A diploid number of 26 was obtained in eight species. Of the remainder, *G. bolusii* was found to have 39 somatic chromosomes and both *G. aspera* and *G. inaequalis* have 52 somatic chromosomes. In all the species examined, the chromosomes were acrocentric, sometimes tending to be submetacentric, and relatively uniform in size, ranging in length from 1,2 to about 2,5μ (fig. 20: A—K). The size was found too uniform to allow recognition of groups of small or large chromosomes. Satellites were sometimes observed on one or two chromosomes of intermediate size. The chromosome numbers found in the genus indicate that the basic number is 13. The karyotype is very similar to that of *Hesperantha* and confirms the view that these two genera are closely related.

There has been only one previous report on the cytology of *Geissorhiza*, when Gwynn (1958) found a diploid number of 26 for *G. aspera* (as *G. secunda*). The present author's findings confirm this number for the genus but not for that particular species. Because polypoloidy was found to be rare in the tribe *Ixieae*, particularly in the species of the winter rainfall region, the occurrence of three polyploid species in *Geissorhiza* caused some surprise. Separate populations from distant localities were therefore examined. The additional populations of *G. aspera*, *G. inaequalis* and *G. bolusii* were found to have the same level of polyploidy as those previously studied. Although meiotic studies were not made, it appears that *G. aspera* and *G. inaequalis* are tetraploid species. They are known to be fully fertile. It is possible that the plant studied by Gwynn was a diploid individual of *G. aspera* or it may have been confused with another species.

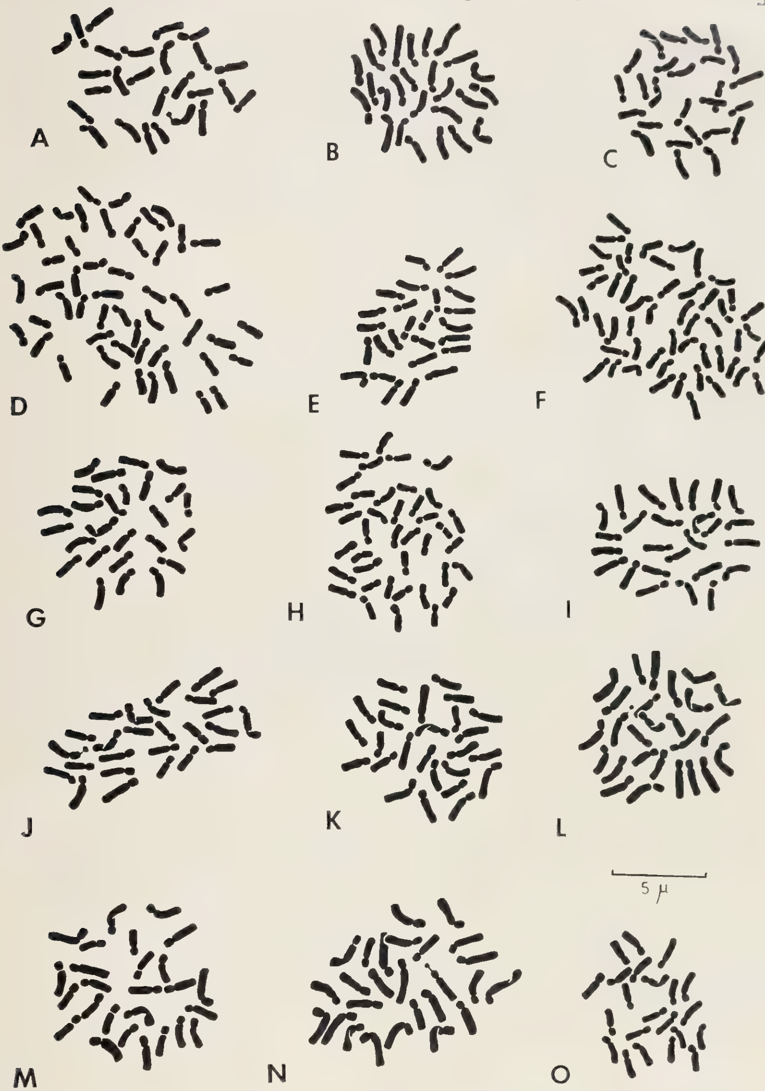

FIG. 20.

Karyotypes of *Geissorhiza*, *Engysiphon* and *Melasphaerula*. A. *Geissorhiza splendidissima;* B. *G. louisabolusii;* C. *G. imbricata;* D. *G. aspera;* E. *G. heterostyla;* F. *G. inaequalis;* G. *G. aff. leipoldii;* H. *G. bolusii;* I. *G. pusilla;* J. *G. nana;* K. *G. ovata;* L. *Engysiphon brevitubus;* M. *E. exscapus;* N. *E. longifolius;* O. *Melasphaerula graminea.*

Geissorhiza bolusii is a sexually sterile species which is similar, and probably identical to *G. rupestris*, another species which does not produce seed. Flowers are sometimes produced but seed is never set. Instead small cormlets are produced in the axils of the bracts on the inflorescence, sometimes after flowering has occurred or in place of the flower. In view of the vegetative apomixis found in this plant, it came as no surprise that it was found to be triploid. Populations from both Bains Kloof and the Cape Peninsula had 39 chromosomes and with the sexual sterility in this plant it is likely to be a naturally occurring triploid species. The cormlets appear to have assumed the function of seeds and are presumably dispersed in a similar way.

ENGYSIPHON

$2n = 26.$

Three species of the small genus *Engysiphon*, a segregate of *Geissorhiza*, were examined (Table 10). The genus, which is found only in the south western Cape, is distinguished from *Geissorhiza* by its larger, usually long tubed flower and its larger asymmetrical corm. All three have a diploid number of 26 and a similar karyotype consisting of rather uniform acrocentric chromosomes which range in size from 1,0 to 2,5μ in length (fig. 20: L—N). The karyotype is indistinguishable from that of *Hesperantha* and *Geissorhiza*, and indicates a close relationship between these genera.

MELASPHAERULA

$2n = 22.$

Melasphaerula is a monotypic genus, widespread in the south western Cape. The plant has a symmetrical corm with hard entire tunics. The scape is highly ramified, and bears large numbers of small, dull coloured zygomorphic flowers. *M. graminea* was found to have a diploid number of 22, with predominantly acrocentric chromosomes more or less uniform in size (fig. 20: O) from 1,3 to 2,0μ in length.

Intergeneric hybridisation

Attempts to obtain intergeneric hybrids in this group of genera were rather unsuccessful (Table 1). A cross between *Geissorhiza leipoldtii* aff. and *Hesperantha falcata* failed, and although *Schizostylis coccinea* hybridised with *Hesperantha falcata*, the number of seeds in the fruit was reduced, and the seed failed to germinate. This is perhaps an indication of a small degree of compatibility between these two genera, and can be regarded as evidence of their suggested close relationship.

Discussion

It is clear that the basic number of *Schizostylis*, *Hesperantha*, *Geissorhiza* and *Engysiphon* is 13 and that they have very similar karyotypes which should be regarded as evidence of their close relationship to one another.

The basic number in *Melasphaerula* is 11 and it is probably not very closely related to the other genera. It has been placed in this section mainly on morphological grounds. *Melasphaerula* is a rather unusual member of the tribe *Ixieae* and does not fit conveniently in any classification of the group. The plant is very branched and has zygomorphic flowers and a peculiar three winged capsule. One feature which indicates its relationship is its corm which has hard entire tunics which in old plants are split and lie on top of the newer tunics. Although the corm tunics resemble those of *Geissorhiza*, the corm is not asymmetric as it is in *Geissorhiza* and its immediate allies.

Taxonomic position of *Schizostylis*

Schizostylis has long been regarded as the probable ancestor of the above group of genera. It has all the floral characteristics of *Hesperantha* but lacks a true corm. Instead, the rootstock is a somewhat short, thick rhizome which has an entire but papery covering. This structure has been regarded as the forerunner of the asymmetrical corm of *Hesperantha* with its entire but woody tunic (Lewis 1954).

Schizostylis produces small propagules which are remarkably like tunicate corms in the axils of the scape. This fact suggests a possible alternative interpretation of the rootstock which may be an expanded corm and rhizome-like as a secondary development. As corms are essentially modified to survive dry conditions it seems a plausible argument that *Schizostylis*, a streamside plant, may have lost its corm due to the semi-aquatic conditions under which it grows. Some species of *Hesperantha* and *Geissorhiza* also grow in marshy places and have retained their corm but in this case the wet area dries out completely during the dry season.

Since the first classification of the Iridaceae by Bentham & Hooker (1883) *Schizostylis*, *Hesperantha*, and *Geissorhiza* have been placed together in the same tribe or subtribe. The only exception to this was made by Hutchinson (1934) who placed *Schizostylis* together with *Aristea* in a tribe quite separate from *Hesperantha* and *Geissorhiza*. The basis for this treatment was the absence of the corm in *Schizostylis*. This has since been refuted by Lewis (1954) on purely morphological grounds because *Hesperantha* and *Schizostylis* are identical except in their rootstock, and as explained above, even this difference is not necessarily fundamental. Indeed, whatever the nature of the rootstock it is quite clear from both morphological and cytological evidence that these two genera are very closely allied, and except for this vegetative difference, would surely be placed in a single genus.

The validity of *Engysiphon*

Engysiphon is a relatively new genus which was described by Lewis (1941) as a segregate of *Acidanthera*, an artificial collection of species grouped together

by Baker (1896). Lewis showed that the South African species placed in *Acidanthera* belonged either to *Gladiolus*, *Hesperantha*, *Tritonia* or were allied to *Geissorhiza*. These latter species she placed in the new genus *Engysiphon*. The genus differs from *Geissorhiza* in having large slightly zygomorphic flowers with long narrow perianth segments. *Geissorhiza* typically has smaller flowers which are actinomorphic. The perianth tube is also far longer in most species of *Engysiphon* than in *Geissorhiza*.

Cytological investigation has shown that Lewis was correct in her treatment of *Acidanthera* for species placed in *Gladiolus* and *Tritonia*, namely *G. praelongitubus* and *T. flabellifolia* were found to have a karyotype resembling those of the rest of the species of the genera to which they were referred. *Engysiphon* has proved to have a basic number of 13 and a karyotype like *Geissorhiza*. In reviewing the validity of many genera in the Iridaceae it seems that *Engysiphon* is hardly sufficiently distinct from *Geissorhiza* to merit recognition, as far greater variation in flower structure occurs in most other genera than exists between *Geissorhiza* and *Engysiphon*. There is little doubt, however, that the distinction is very convenient because *Geissorhiza* is a large genus and the identification of species in this group is already very difficult.

Conclusion

The present study confirms Lewis' classification of the five genera in this section. She placed the four genera which have a basic number of 13 in a single phylogenetic line beginning with *Schizostylis* and leading to *Hesperantha* and then independently to *Geissorhiza* and *Engysiphon*, where a small degree of zygomorphy is achieved in the flower. She placed *Melasphaerula* at the end of a separate line separating quite early from the main sequence leading to *Geissorhiza*. Lewis continued her line from *Geissorhiza* to *Gladiolus* and its allies for she believed that *Gladiolus* was derived from *Geissorhiza* and that the two genera actually merged together. This will be discussed later under *Gladiolus*.

Melasphaerula does not fit in the same phylogenetic line but the nearest related genus appears to be *Geissorhiza*. It is more specialised than *Geissorhiza* in that the flowers are zygomorphic. Also the capsule is rather different from the fruits in the remainder of the tribe.

Lewis placed all these genera together with *Dierama*, *Ixia*, *Tritonia* and their allies in her subtribe *Ixiinieae*. She did not divide up this large subtribe further for she remarks that further subdivision would result in artificial grouping of genera. The karyological results do, however, refute this statement and have shown that within Lewis' *Ixiinieae* there are several distinct karyotypes each one usually shared by a group of genera which are morphologically similar. *Schizostylis*, *Hesperantha*, *Geissorhiza* and *Engysiphon* form a natural unit, all having a karyotype with 26 chromosomes and can conveniently be grouped

in a separate subtribe which the present author proposes to name *Hesperanthineae. Melasphaerula* does not fit perfectly into this subtribe but rather than create a separate subtribe for a single species it has been placed here in the group to which it seems most closely related.

TABLE 11
Chromosome numbers in *Romulea* and *Syringodea.*

Species	Diploid No.	Collection Data or Reference
ROMULEA Maratti		
R. hantamensis (Diels) Goldblatt	30	Calvinia, C.P. *Goldblatt 276*
R. sabulosa Beg.	26	Nieuwoudtville, C.P. *Goldblatt 96* (J)
R. minutiflora Klatt	26	Krom River, Cedarberg, C.P. *Goldblatt 230*
R. flava (Lam) de Vos	24	Simonsberg, C.P. *Goldblatt 41* (J)
(as R. bulbocodioides)	18	(Gwynn 1958)
R. ochroleuca unpublished name	18	(Gwynn 1958)
R. rosea Eckle	18	(Gwynn 1958)
R. rosea var. parviflora Bak.	18	Stellenbosch, C.P. *Goldblatt 138* (J)
R. atrandra var. luteoflora de Vos	22	Calvinia, C.P. *Goldblatt 277*
R. triflora (Burm, f.) N.E. Br.	20	Ceres district, C.P. *Goldblatt 317*
R. columnae (as R. parviflora)	60	Matsuura and Suto (fide Darlington and Wylie 1955)
R. bulbocodium	34	Fernandes et al. (fide Darlington and Wylie 1955)
(The large number of species examined by de Vos 1965 is not included here)		
SYRINGODEA Hook. f.		
S. longituba (Klatt) O. Kuntze	12	Albany district, C.P. *Bayliss 2182* (NBG)
S. montana Klatt	12	Giftberg, C.P. *Barker 10210* (NBG)
S. unifolia Goldblatt (ined.)	22	Matroosberg, C.P. *Stayner s.n.* (NBG 87602)

All localities are in the Cape Province (C.P.), South Africa. Unless otherwise stated, specimens are located at the Bolus Herbarium, Cape Town.

d. Subtribe ***Crocineae***
Romulea, Syringodea, Crocus

This group comprises small plants which have reduced inflorescences. The flowers are reduced to one per branch of the inflorescence, and often the aerial part of the scape is so reduced that the ovary is subterranean. The corms are either hard and woody, or somewhat papery, but entire, the leaves terete to bifacial and the flowers actinomorphic, usually with modified style branches.

ROMULEA

$2n = 30—18.$

Romulea is a large genus of approximately ninety species occurring from the Mediterranean, along the mountains of Africa to the Cape where most species are found. The genus consists of small reduced plants, the inflorescence

of which can be regarded as solitary flowered, although the scape is often branched. The corms are small, with hard woody tunics and are often very characteristically shaped. The leaves are very distinctive in this genus, being slender, terete or sub-terete and having four channels running the length of the leaf. The flowers are actinomorphic often brightly coloured and usually short-tubed though some species have a perianth tube as long as five centimetres. The three style branches are usually deeply forked.

Romulea is one of the few genera in the *Iridaceae* in which the chromosome cytology has been extensively studied (de Vos 1965). Accordingly, only a few species were studied (Table 11) by the present author and a range of somatic chromosome numbers from 18 to 30 was found in these few species. The chromosomes are acrocentric and of comparable size in all the species examined, although somewhat smaller in species with a high chromosome number. There is little marked difference in size between the chromosomes of any species so that no distinctive karyotypes could be recognised (fig. 21: A—G).

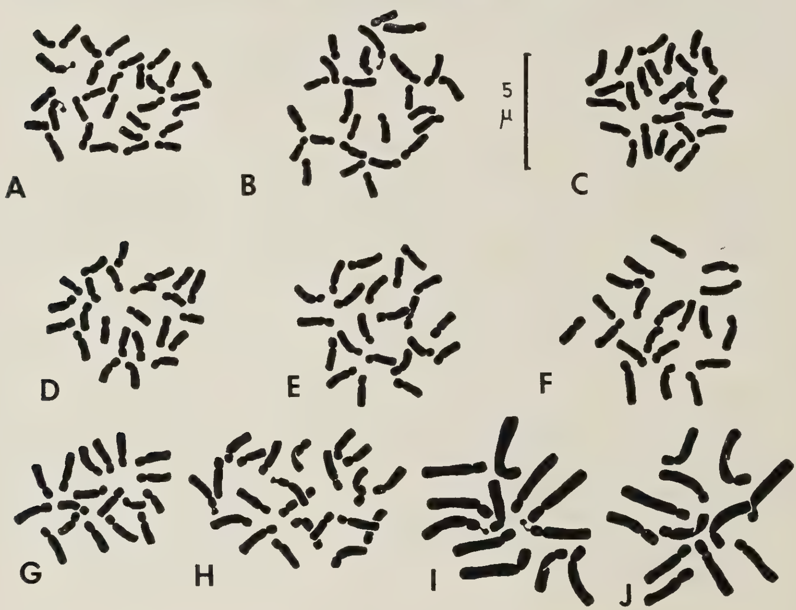

FIG. 21.
Karyotypes of *Romulea* and *Syringodea*. A. *Romulea hantamensis;* B. *R. sabulosa;* C. *R. minutiflora;* D. *R. flava;* E. *R. atrandra var. luteoflora;* F. *R. triflora;* G. *R. rosea var. parviflora;* H. *Syringodea rosea;* I. *S. longituba;* J. *S. montana.*

De Vos (1965) examined more than forty species and varieties including all but two of the species studied by the present author. Only the counts of 30 in *R. hantamensis* and 20 in a plant referred to *R. triflora* are new records for the genus. The counts for four of the other species confirm the results of de Vos but the present author obtained a diploid number of 22 in *R. atrandra* var. *luteoflora* while de Vos reported 2n = 20 for this variety although she found 2n = 22 in *R. atrandra* var. *atrandra*. An earlier cytological report for *Romulea* is that of Gwynn (1958) who found 2n = 18 in *R. rosea*, *R. ochroleuca* and *R. flava* (as *R. bulbocodioides*). This latter record is the only one not confirmed by de Vos. She found 2n = 24 in several varieties of *R. flava* (as *R. bulbocodioides*). It seems likely, with the difficulties of identification in *Romulea* that Gwynn was dealing with another species. Other records in *Romulea* are 2n = 60 for *R. parviflora* (apparently a synonym of *R. columnae*, a Mediterranean species), by Matsuura and Suto (fide Darlington & Wylie 1955), and 2n = 34 for *R. bulbocodium* (also a Mediterranean species) by Fernandes *et al.* (fide Darlington & Wylie 1955).

It is clear from these cytological studies that *Romulea* is a heteroploid genus. Apart from a few polyploid species which have chromosome numbers of 44 and 54 there is an aneuploid series ranging from 2n = 18 to 34. The majority of species in this series have a diploid number of 24 but several species have numbers of 26, 22 and 18.

The genus is still being studied by de Vos and was thus not investigated in any detail by the present author. It is, however, clear from the work of de Vos that cytology is proving an extremely valuable tool in resolving the many problems in this genus in which the taxonomy is notoriously difficult.

SYRINGODEA

2n = 22, 12.

Syringodea is a small genus known only from southern Africa. It appears to be related to *Romulea*, but the plants are more reduced, the flowers are fugaceous, usually solitary and an aerial stem is lacking. Unlike *Romulea* the terete leaves lack the grooves typical of that genus.

Three of the approximately ten species in the genus were studied (Table 11). The chromosomes are amongst the largest in the tribe *Ixieae*. One species, *Syringodea unifolia* has a diploid number of 22 and here the chromosomes are typical of the *Ixieae* in size and shape. In the two species with a diploid number of 12, the chromosomes are larger and almost of a size found in the *Irideae*, which are characterised by large chromosomes (fig. 21: H—J).

The genus *Syringodea* has not previously been examined cytologically. Like *Romulea* it appears to be heteroploid and until more species can be studied nothing can be said of the chromosome evolution in the genus. The comparatively

large size of the chromosomes in *S. longituba* and *S. montana* are unusual and are largest in the tribe *Ixieae*. It is likely that they are the end result of decreasing aneuploidy. If so it would be expected that individual chromosomes would increase in size to prevent the loss of genetic material.

The taxonomic position of *Syringodea unifolia*.

Syringodea unifolia is an extremely unusual species. It has several characteristics which make it appear misplaced in its present genus. *Syringodea*, as generally accepted, comprises several small reduced plants with an almost symmetrical corm with woody tunics and a rosette of several slender, terete or sub-terete leaves. The flowers lack an aerial stem or peduncle and are raised above the ground by a long slender perianth tube. The flowers are usually small and soft textured and the style is divided into three short branches. The above species differs in most of these features. The corm is flattened in a vertical plane, being lens shaped with a crescent shaped ridge forming the periphery of the lower part of the lens. The plant bears a single, rather succulent terete leaf and the flower, though long tubed, is very large for the genus. Most unusual of all, the three style branches are themselves irregularly branched and divided.

This type of style is found in the genus *Crocus* (Maw 1882) and in one species of *Romulea* where bifid stigmas are the rule. The rather distinctive corm is characteristic of *R. tortuosa* and is not known in either *Crocus* or *Syringodea*. Argument can thus be led for transferring *Syringodea uniflora* to *Romulea*, for although a short perianth tube is the more usual of this genus, several species have a long tube and lack an aerial peduncle. An equally strong case can be made for the inclusion of this species in *Crocus*, where the peculiar shaped corm is the only difficulty. The leaf and flower are very characteristic of *Crocus* as is the stigma.

Cytological study does not appear to help in establishing the correct position or the plant. The small chromosomes are like those found in *Romulea* but the diploid number is quite different from *R. tortuosa* ($2n = 30$), the only plant that seems to have a similar corm. Too little is as yet known about the cytology of *Syringodea* but again the karyotype differs greatly between the two species studied here and *S. unifolia*. If *S. unifolia* is to remain in its present genus then both *Romulea* and *Syringodea* must be viewed in rather different terms. At present the main and diagnostic difference between these two genera is said to be the nature of the style branches; either entire in *Syringodea* or bifid in *Romulea* (Lewis 1954; Burtt 1967). The diagnostic character which now seems more significant is the leaf, being sub-terete in *Syringodea* and four-channelled in *Romulea*.

It is quite clear that all the other characters overlap, and it seems to indicate that *Syringodea* is probably a very specialised and reduced genus derived from *Romulea*. In an expanded definition of the genus, *S. unifolia* can then remain in its present position.

The subtribe *Croceae* sensu Bentham & Hooker.

Romulea and *Syringodea* are a pair of related genera which are both very reduced in size. In most species of *Romulea* only the pedicel extends above ground. In *Syringodea* this reduction has proceeded a step further for here the perianth tube serves to raise the flower above ground level. This reduction of the inflorescence and general size of the plant occurs in two other genera of the Iridaceae, namely *Galaxia* and *Crocus*, and this feature prompted Bentham & Hooker to group them together in a single subtribe which they placed in their tribe *Sisyrinchieae* together with *Aristea* and *Bobartia*. Pax (1888) raised this subtribe to the rank of subfamily but other workers followed Bentham & Hooker's concept. Hutchinson also recognised this grouping and made it one of his eleven tribes.

It remained to Lewis (1954) to point out the true affinities of these four genera. She shows clearly that *Galaxia* is actually allied to *Homeria* for it has a corm and leaves like *Moraea* and *Homeria*. The reduced size and inflorescence can thus be regarded as a case of parallel evolution. Lewis believed that *Romulea* and *Syringodea* were related and that they belonged in the tribe *Ixieae*, for though rather modified in many features, they have a corm very like that in *Hesperantha* and *Geissorhiza*. Both these suggestions made by Lewis are confirmed by cytological observations, for as explained earlier, *Galaxia* has the large chromosomes typical of the tribe to which *Moraea* and *Homeria* belong, while *Romulea* has small chromosomes which are typical of the *Ixieae*. *Syringodea* has chromosomes which are comparatively large but still appear to belong to the group with small chromosomes.

The taxonomic affinities of *Crocus*

The taxonomic position of *Crocus* is somewhat doubtful. Plants in this genus, like *Romulea* and *Syringodea*, are very reduced and they have no aerial stem or peduncle. The genus which is Mediterranean and Middle Eastern in distribution, is believed to be derived from *Romulea* which is both African and Mediterranean in distribution (Burtt 1967). *Crocus* appears better referred to the *Ixieae* as it has the type of corm found in this tribe. However, few species of *Crocus* have the peculiar hard, woody asymmetric corm tunic found in *Romulea* and *Syringodea*. Also *Crocus* has a leaf which is bifacial whereas the leaf is sub-terete in *Syringodea* and in *Romulea* is monofacial and peculiar in being four-grooved. These and other morphological features indicate that if

Crocus is derived from *Romulea* or *Syringodea* it has since become very modified and that the relationship between them is not as clear as suggested by Lewis and by Burtt.

Crocus is another genus where the cytology has been quite well investigated. The studies of Mather (1932), Karasawa (1956), Feinbrun (1958) and others have revealed that it is karyologically very complex. There is a series of somatic numbers ranging from 6 to 30, but it is probable that both aneuploidy and polyploidy have occurred in the evolution of the genus. Species with the higher somatic numbers have smaller chromosomes which resemble somewhat those of most Ixioid genera in general appearance and size but those with low somatic numbers have very large chromosomes resembling the *Irideae*.

A diploid number of 8 has been suggested by Feinbrun as the ancestral number in *Crocus* on the grounds that 8 and multiples of 8 are the most common diploid numbers in the genus. Apart from the fact that it is perhaps easiest to derive all the reported somatic numbers from 8 there is no support for this hypothesis. Unfortunately, it is not possible as yet to assign a primitive position in the genus to any particular species or group of species.

All that can be said in our present state of knowledge is that if *Crocus* belongs to the *Ixieae* and was evolved from a *Romulea*-like plant, then species with the higher somatic numbers and smaller chromosomes probably represent the ancestral condition. Consequently species with lower somatic numbers and large chromosomes are derived from them and are advanced at least in their karyotype. This is merely hypothetical and the condition in *Crocus* is open to many other interpretations. If Feinbrun's suggestion is correct, however, then on cytological grounds the position of *Crocus* in the tribe of *Ixieae* is seriously challenged.

Further morphological and cytological study of *Crocus* is indicated, perhaps by European workers who can more easily obtain species in their natural state. Tentatively, it is suggested that the subtribe *Crocineae* (as *Croceae*) of Bentham & Hooker (*Romulineae* as proposed by Lewis), containing *Romulea, Syringodea* and *Crocus* be maintained until more information is discovered.

The origin of the *Crocineae*

Romulea and its reduced allies are presumably derived from a less specialised group with similar but less reduced characteristics. *Hesperantha*, *Geissorhiza* and *Engysiphon* are the only genera with an asymmetric corm like that found in *Romulea*, which is clearly the least modified genus in the *Crocineae*. In addition, the peculiar four-grooved leaf of *Romulea* occurs in species of *Geissorhiza* and *Engysiphon* where it becomes clear that this type of leaf is derived from the ordinary equitant type by a thickening of the margins and the region round the mid-vein. The unthickened portions thus form the grooves. Species

of *Geissorhiza* also have relatively unspecialised flowers with a short perianth tube like those occurring in most species of *Romulea.*

Thus *Geissorhiza* has a strong claim to be very like the ancestor of *Romulea.* It is interesting to note that in both *Geissorhiza* and *Hesperantha* there are species in which the inflorescence is reduced to a solitary flower. In *Geissorhiza*, these species differ from *Romulea* in the possession of a simple stigma in contrast to the bifid stigmas in *Romulea.*

If a plant resembling a *Geissorhiza* is accepted as the ancestor of *Romulea* and thus of the *Crocineae*, several comments can be offered on the evolution of the karyotypes in *Romulea.* The somatic number in *Geissorhiza* and all its close relatives is 26 and a similar number can then be expected in the ancestral or least specialised species of *Romulea.*

The work of de Vos has shown that the chromosome number in *Romulea* is closely correlated with the appearance of the corm which varies considerably thoughout the genus. The simplest corm and the one from which all others are most easily derived is, according to de Vos, the kind found in *R. flava* and she suggests that this is the most primitive type. This contention is supported by the morphology of the plant for *R. flava* is a species in which the scape is often borne above ground though the flowers are still solitary on the branches. The somatic number in *R. flava* and others with this kind of corm is 24, a number close to that of *Geissorhiza.* Although a diploid number of 26 occurs in a few species of *Romulea*, 24 is far more common and as this number is correlated with putatively primitive characters it appears that this is the ancestral condition in the genus. Consequently a basic number of 12 is suggested for *Romulea.* Accepting this, it is clear that both ascending and descending aneuploidy have occurred though the latter has predominated, which is in accordance with the view of Stebbins (1950) that this is more common than increasing aneuploidy.

e. Subtribe ***Gladiolineae***

Gladiolus, *Acidanthera*, *Radinosiphon*, *Homoglossum* (including *Petamenes*), *Oenostachys* and *Anomalesia* (including *Kentrosiphon*).

This complex consists of small to medium sized, herbaceous deciduous plants. The plants have a spherical to flattened, symmetrical corm with entire, but fairly soft papery tunics, although the old, outermost tunics often split and appear fibrous. The inflorescences are, with few exceptions secund and the seed is winged except in a few isolated species and in *Radinosiphon.* The flowers are large and colourful, usually zygomorphic and the three style branches are typically expanded and bilobed at the apex. Two genera, *Petamenes* and *Kentrosiphon*, are reduced to synonymy, being included in *Homoglossum* and *Anomalesia* respectively.

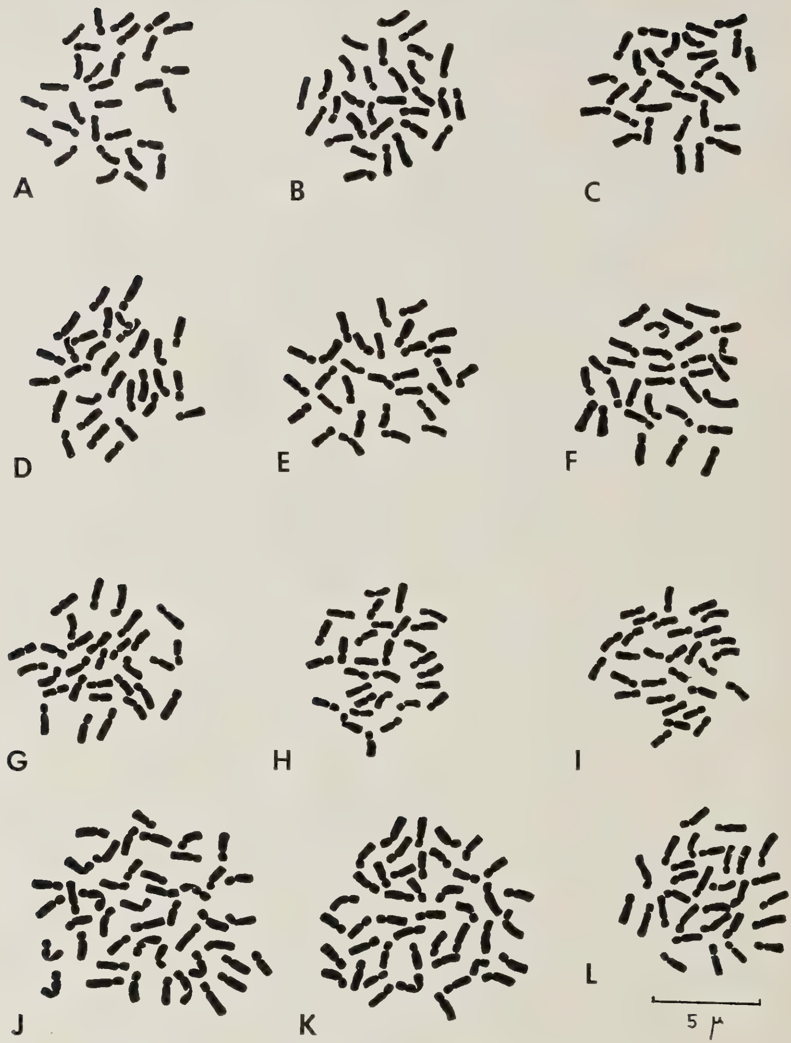

FIG. 22.

Karyotypes of *Gladiolus* and *Radinosiphon*. A. *Gladiolus pritzellii;* B. *G. undulatus;* C. *G. ceresianus;* D. *G. guinzii;* E. *G. brevifolius;* F. *G. edulis;* G. *G. crassifolius aff.;* H. *G. varius;* I. *G. praelongitubus*, J. *G. natalensis* (*psittacinus*), K. *G. natalensis var. cooperi;* L. *G. buckerveldii* (previously *Petamenes buckerveldii*).

TABLE 12
Chromosome Numbers in *Gladiolus*.

Species	Diploid No.	Collection Data or Reference
GLADIOLUS L.		
G. tristis L.	30	(Bamford 1935)
	30	(Mensinkai 1939)
G. pritzellii Diels	30	Nieuwoudtville, C.P. *Goldblatt 257*
G. undulatus Jacq.	30	Cedarberg, C.P. *Goldblatt 309*
	30	(Bamford 1935)
G. buckerveldii (L. Bol.) Goldblatt	30	Algeria, Cedarberg, C.P. *Jackson sn.* (NBG 85913)
G. ceresianus L. Bol.	30	Cold Bokkeveld, C.P. *Goldblatt 267*
G. gueizii (Kunze) Lewis	30	Cape St. Francis, C.P. *Basson s.n.* (NBG 88091)
G. brevifolius Jacq.	30	Kirstenbosch, C.P. *Goldblatt 523*
	30	(Bamford 1935)
G. edulis Burch ex Ker	30	Alice, Eastern C.P. *Goldblatt 369*
G. crassifolius Bak.	30	Mt. Anderson, Tvl. *Goldblatt 63* (J)
	30	(Bamford 1935)
G. varius Bol. f.	30	Graskop, Tvl. *Goldblatt 80* (J)
G. praelongitubus Lewis	30	Mt. Anderson, Tvl. *Goldblatt 64* (J)
G. natalensis (Eckl.) Reinw. ex Hook (=G. psittacinus)	45, 60, 75.	Inhaca Island, Mozambique. *Goldblatt 524* (J)
(as G. psittacinus)	90	(Bamford 1935)
G. natalensis var. cooperi Bak.	45, 60, 75.	Haenertsburg, Tvl. Raised from seed.
G. primulinus Bak.	60	(Bamford 1935)
	60	(Mensinkai 1939)
(n=30)		(Vilmorin and Simonet 1927)
G. dracocephalus Hook	90	(Bamford 1935)
	80	(Mensinkai 1939)
G. byzantinus Mill (n=30)		(Vilmorin and Simonet 1927)
	90	(Bamford 1935)
	60	(Mensinkai 1939)
G. illyricus Koch	90	(Bamford 1941)
	60	Portinho, Portugal (Hamilton 1968)
G. segetum Ker	120	(Bamford 1935)
	171±2	El Ronquillo, Spain (Hamilton 1968)
G. communis L.	±138	(Bamford 1935)
	180	(Bamford 1941)

(The large number of species studied by Bamford (1935; 1941) are not listed here.)

All localities are in South Africa unless otherwise stated. The provinces are abbreviated as follows: Cape Province—C.P.; Transvaal—Tvl. Specimens are housed in the Bolus Herbarium, Cape Town, unless stated to the contrary.

GLADIOLUS

$2n = 30, 45, 60.$

Gladiolus is one of the largest genera in the Iridaceae, comprising about 150 species. It is distributed from southern Europe, through the Mediterranean region into Africa. The majority of species occur in southern Africa with the greatest concentration in the winter rainfall region. The variation in the flower is considerable, ranging from actinomorphic to extremely zygomorphic species. It is one of the few in which the cytology has been intensively studied. Eleven

species were examined by the present author, ten of which were found to have a diploid number of 30 (Table 12). The exception is *G. natalensis*, two varieties of which are polyploid and have chromosome numbers of 45, 60 and 75. The karyotypes are very uniform in all species, and the chromosomes are all small and acrocentric to submetacentric. The length of the chromosomes ranges from 1 to 2μ (fig. 22). The karyotype lacks distinguishing characteristics so that the diploid number and general size of the chromosomes are the only features of note. Satellites, which must be present, are seldom observed, and cannot be ascribed to any particular chromosome pair.

TABLE 13

Chromosome Numbers in *Acidanthera, Radinosiphon Homoglossum* and *Anomalesia*.

Species	Diploid No.	Collection Data or Reference
ACIDANTHERA		
A. bicolor Hochst	30	East Africa (ex hort) *Goldblatt 10* (J)
	30	(Sharma and Talukdar 1960)
A. aequinoctialis Bak.	30	Kanabali, Sierra Leone (Harvey 1966)
HOMOGLOSSUM Salisb.		
H. merianellum (L.) Bak. . . .	30	Silvermine Plateau, C.P. *Goldblatt 389*
H. watsonium (Thunb.) B.N.E.Br.	30	C.P. (ex hort) *Goldblatt 17* (J)
(as Gladiolus)	30	(Bamford 1941)
(as Gladiolus)	66	(Sharma & Talukdar 1966)
H. priori N.E. Br.	30	Fish Hoek, C.P. *Goldblatt 495*
H. abbreviatus (Andr.) Goldblatt	30	Botrivier, C.P. *Goldblatt 292*
RADINOSIPHON N.E. Br.		
R. cf. leptostachya N.E. Br. . . (only seed & corms seen)	30	Chimanimani Mountains, Rhodesia (raised from seed, flowers not seen)
R. leptostachya N.E. Br. . . .	30	Mt. Anderson, Tvl. *Goldblatt 600*
ANOMALESIA N.E. Br.		
A. cunonia (L.) N.E. Br. . . .	30	Glencairn, C.P. *Goldblatt 481*

All localities are in South Africa unless otherwise stated. Cape Province is abbreviated—C.P. Unless stated to the contrary all specimens are located in the Bolus Herbarium, Cape Town.

Two varieties of the summer rainfall area species, *G. natalensis* (*G. psittacinus*) were examined (fig. 22: J, K). In both cases wild populations were studied and were found to be cytologically heterogeneous. Multiples of 15 chromosomes were observed, ranging from 45 (triploid) to 75 (pentaploid). No diploid individuals were found.

As already mentioned, the cytology of *Gladiolus* has been quite extensively investigated. The results of a number of studies in this field were reviewed by Bamford (1935), who supplemented the existing work with many new chromosome counts (Bamford 1935; 1941).

From the approximately forty species studied by that date, both by Bamford and earlier workers, the following conclusions emerged. The basic number in the genus is 15 and the majority of species are diploid. As a whole the genus is heteroploid with somatic numbers ranging in multiples of 15 from 30 to 120 and higher. When arranged according to their geographical distribution, an interesting pattern emerged from the cytology of the species studied. The species occurring in the winter rainfall area of South Africa are all diploid (2n = 30). The tropical and southern African species of the summer rainfall area range from diploid through to hexaploid (2n = 90), while the European and Asian species are all high polyploids with somatic numbers of up to 180 having been recorded.

Unaware of Bamford's work, Mensinkai (1939) proposed an alternative interpretation of the cytology of *Gladiolus*. He found somatic numbers of 30, 60 and 80 in the few species he studied. On the basis of this and a meiotic study in which some irregularities were observed, he postulated that the basic number in *Gladiolus* was 10 and that species having a somatic number of 30 were triploid. In the light of present knowledge this interpretation must be disregarded.

The few cytological observations published after 1941 (fide Hamilton 1968) and the work of the present author confirm Bamford's conclusions. The six winter rainfall species studied here are diploid. Of these, the counts for *G. pritzellii*, *G. queizii*, *G. buckerveldii* and *G. ceresianus* are new records while those for *G. undulatus* and *G. brevifolius* confirm earlier findings. Five summer rainfall species were studied and as expected both diploid and polyploid species were found. Of the four which are diploid, namely *G. edulis*, *G. varius*, *G. praelongitubus* and *G. crassifolius*, the first three are new records and the last, that of *G. crassifolius*, confirms an earlier report. The counts for *G. natalensis* also confirm previous reports of its polyploid nature.

The position of *Gladiolus buckerveldii*.

This species, originally referred to *Antholyza*, then transferred to *Petamenes* by N. E. Brown, has been placed in *Gladiolus* by the present author. The grounds for this name change are dealt with fully in the discussion of the genera *Homoglossum* and *Petamenes*, and the taxonomic treatment is presented in a separate chapter dealing with all the name changes.

Heteroploidy in some species of *Gladiolus*.

One interesting feature which has emerged from the more recent studies is that several species appear to be heteroploid. Reports for *G. byzantinus* and *G. illyricus* give somatic numbers of both 60 and 90, and numbers of 120 and ±171 are recorded for *G. segetum*. Previous reports for *G. natalensis* (as *G. psittacinus*) were 2n = 90 (Bamford 1935), in which the present author found somatic numbers of 45, 60 and 75 in single wild populations of two varieties of this species.

Apomixis seems to be unlikely, for *G. natalensis* is reported to hybridise easily with other species and is believed to be one of the ancestors of the cultivated forms of *Gladiolus* which are usually tetraploid. A reduction in fertility would be expected in the triploid and pentaploid individuals due to meiotic abnormalities and this has been observed in many of the cultivated plants of *G. natalensis*. The occurrence of triploid individuals is remarkable as it suggests the presence of diploid plants which presumably hybridised with a tetraploid to yield the triploids. Diploid members of this species have, however, yet to be discovered, but a search for these may be rewarding. Another explanation of the presence of triploids and pentaploids is as follows. Populations may usually be either hexaploid or tetraploid, but where these two groups overlap in distribution, hybridisation would result in pentaploid plants. Abnormal meiosis would occur in these and could conceivably result in the production of haploid gametes. These when hybridised with a tetraploid could also produce the triploid individuals that were observed. It is, however, clear that populations of *G. natalensis* require further study and should produce interesting results.

The origin of *Gladiolus*

The occurrence of an increase in ploidy with distance from the Cape winter rainfall area seems to indicate a southern origin for the genus *Gladiolus* for it is clear that the diploid species could not be derived from the more northern polyploids. This hypothesis, which does not seem to have been mentioned previously, is supported by the occurrence of what are regarded as the most primitive species in the genus, with actinomorphic flowers, growing only in the south western Cape Province (Lewis 1954). The majority of species of *Gladiolus* have zygomorphic flowers and are thus regarded as more specialised.

It must be noted, however, that some diploid species of *Gladiolus* and related genera occur even north of the equator and could have given rise to the diploid species in the Cape Province. If this is correct then the actinomorphic species may not be primitive but specialised. The theory of the southern origin of *Gladiolus* seems the more acceptable.

The ancestry of *Gladiolus*

Geissorhiza has been proposed as the ancestor of *Gladiolus* (Lewis 1954). The reasons for this suggestion are the similarities between the least specialised species of *Gladiolus* and *Geissorhiza*. The woody, split, overlapping tunics of *Geissorhiza* occur in many species of *Gladiolus*, notably the least specialised amongst which are the actinomorphic species *Gladiolus stellatus*, *G. tenellus*, *G. quadrangulus* and *G. citrinus*. These species are recognised as belonging to

Gladiolus mainly by their winged seeds, these being globose in *Geissorhiza*, but in other respects the similarities are such that some authors have placed *Gladiolus stellatus* and *G. quadrangulus* in *Geissorhiza*.

The difference in the karyotypes of the two genera, *Gladiolus* having 15 and *Geissorhiza* 13 as the basic number, indicates that the relationship is not as close as the morphological evidence indicates. If the ancestral position of *Geissorhiza* is correct, *Gladiolus* would have had to originate by a process of increasing aneuploidy. The intermediate basic number of 14 has not been found in either genus but a study of the actinomorphic *Gladiolus* species not yet examined may provide the link. It must be noted that attempted crosses between the two genera made by the present author did not succeed (Table 1) and it is likely that *Gladiolus* and *Geissorhiza* have diverged to such an extent (assuming Lewis' suggested ancestry of *Gladiolus*) that they are no longer compatible. Again, hybrids between the actinomorphic species of *Gladiolus* and *Geissorhiza* may prove the exception and crosses between these should be attempted if possible.

ACIDANTHERA

2n = 30.

One species of this small tropical African genus, which is allied to *Gladiolus*, was studied here. It differs from most species of *Gladiolus* in having subequal perianth segments and broad, rather soft textured leaves. The diploid number is 30 and the karyotype is very similar to that of the diploid species of *Gladiolus*.

Two species of *Acidanthera* have previously been cytologically studied (Table 13), both having 2n = 30, thus the count for *A. bicolor* by the present author is confirmatory (fig. 23: G). The karyotype of this species is very similar to that of the diploid species of *Gladiolus* (fig. 22). This similarity is significant because *Acidanthera* is a genus of rather doubtful validity.

The genus *Acidanthera* was based on the tropical species, *A. bicolor* described by Hochstetter (1845). Baker (1896), however, considered the genus widespread throughout Africa and included in it several discordant elements. Baker's misinterpretation was corrected by Lewis (1941) when she transferred the South African species to *Gladiolus*, *Engysiphon* or *Tritonia*. The tropical African species, which most resemble the type species, are all similar to *Gladiolus*. *Acidanthera* (sensu stricto) is distinguished from the tropical African species of *Gladiolus* by the nature of the perianth segments which are subequal in *Acidanthera* but unequal with the lower segments small and the posterior segment larger and hoodlike in *Gladiolus* (Baker 1896). The distinction does not hold when South African species of *Gladiolus* are taken into consideration because several species have a flower like *A. bicolor*, e.g. *G. tristis*, *G. undulatus* etc.

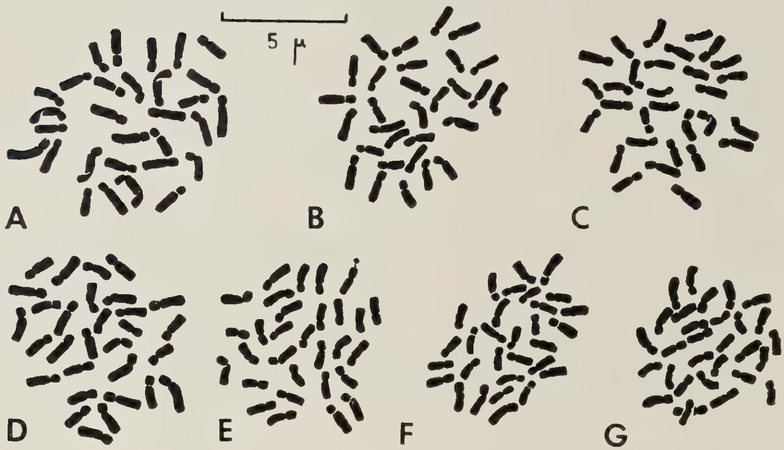

Fig. 23.
Karyotypes of *Homoglossum* (including *Petamenes*), *Acidanthera*, *Radinosiphon* and *Anomalesia*. A. *Homoglossum priori;* B. *H. watsonium;* C. *H. merianellum;* D. *H. abbreviatus;* E. *Anomalesia cunonia;* F. *Radinosiphon leptostachya;* G. *Acidanthera bicolor.*

The fact that species of *Acidanthera* and *Gladiolus* have been crossed successfully confirms the morphological and cytological evidence of the close relationship of the two. There are several records of *Gladiolus-Acidanthera* hybrids (Hamilton 1968; Wright 1966) and these "Gladanthera" hybrids are becoming known in horticulture.

As the evidence shows that there are neither morphological nor cytological grounds for maintaining *Acidanthera*, this genus must be incorporated in *Gladiolus*. In spite of this decision, the author recognised *Acidanthera* provisionally, and has refrained from making the necessary name changes until the genus as a whole can be dealt with.

RADINOSIPHON

$2n = 30.$

Radinosiphon is a small, rather poorly understood genus occurring mainly in the eastern mountains of southern Africa. A diploid number of 30 was obtained in *R. leptostachya*, the one species studied here. The karyotype resembles that of a diploid *Gladiolus*, having rather uniform small acrocentric chromosomes (fig. 23: F).

The diploid number in this genus, described here for the first time, is 30. The karyotype consisting of small, uniform chromosomes points strongly to a close relationship with *Gladiolus*. *Radinosiphon* was believed by Lewis (1954) to be allied to *Gladiolus*. Species of *Radinosiphon* broadly resemble a *Gladiolus*, but its flowers are rather small and the perianth segments subequal. Unlike most species of *Gladiolus* and its allies, it does not have winged seeds. This feature is however shared by some of the European species of *Gladiolus*.

The cytological evidence confirms Lewis' suggestion that the genus is allied to *Gladiolus* but little more can be said of the nature of the relationship. The genus clearly requires further morphological and cytological study before any conclusions can be drawn. Attempts to raise intergeneric hybrids between *Radinosiphon* and *Gladiolus* may also provide valuable information determining their relationship.

HOMOGLOSSUM, PETAMENES (now included in *Homoglossum*), *OENOSTACHYS ANOMALESIA, KENTROSIPHON*, (now referred to *Anomalesia*).

2n = 30.

These five genera are all allied to *Gladiolus* and can conveniently be discussed together. Although not all authors consider these genera to form a natural group with *Gladiolus*, evidence will be led to indicate that these comprise a single entity. The genera are all distinguished from *Gladiolus* and one another by various modifications of the perianth segments. The flowers become increasingly zygomorphic and tend to hide the natural affinities of these genera.

Cytology

Three of the approximately twelve species of *Homoglossum*, two of about eight species previously regarded as *Petamenes*, and one of the three species of *Anomalesia* were studied. All were found to have a similar karyotype in which the diploid number is 30 (Table 13). As in species of *Gladiolus*, *the* karyotype is undistinguished and consists of small acrocentric chromosomes which range in size from 1—2μ (fig. 23: A—E).

There have been only two previous chromosome counts in this group of genera, both for *H. watsonium* but published as Gladiolus, by Bamford (1941) who reported a diploid number of 30 while Sharma and Tulakdar (1960) found a somatic number of 66 in three cultivated forms of the plant they referred to *G. watsonius*. The count for *H. watsonium* by the present author confirms Bamford's finding. The counts for the other three species reported here are new records and indicate that the diploid number for *Homoglossum* is 30. It appears in the light of present results that the plant which Sharma and Talukdar investigated must have been misindentified. The counts for the species previously placed in *Petamenes* and for *Anomalesia* are new cytological records.

Intergeneric hybridisation

The genera under discussion are one of the few groups in the Iridaceae in which intergeneric hybrids can easily be produced. Hybrids between *Gladiolus* and *Homoglossum* are well known. Crosses between *G. tristis* and *H. watsonium* have been recorded by Bamford (1941) and recently by Ingram (1967). This hybrid which is known by the name "Homoglad" is fertile and produces fertile, vigorous offspring. The same cross has been made by the present author. Many amateur gardeners have made crosses between these two genera including Loubser (personal communication) who has reported that he has crossed several other species of *Homoglossum* and *Gladiolus*. There are also several records of natural hybrids occurring between *G. maculatus* and *H. watsonium*, which flower at the same time and in the same locality (Marloth 1915; *Judd sn.* BOL 30675).

Hybrids have also been produced between *Gladiolus* and *Anomalesia*, between *Gladiolus* and *Petamenes* (sensu lato) and between *Anomalesia* and *Kentrosiphon* (Table 1). Thus the genera appear to be interfertile amongst themselves as well as with *Gladiolus*.

Although not all the possible intergeneric crosses in this group have been made, the evidence strongly suggests that these will prove successful. At present the evidence is sufficiently strong to point to a close relationship among all the genera in this group. Likewise, those species which have been examined cytologically all exhibit a similar karyotype, another indication of close relationship. It is unfortunate that more species could not be found for cytological investigation, particularly among the several tropical African species of *Petamenes* now regarded as *Oenostachys*, the two recognised species of *Oenostachys* and *Anomalesia saccata*, previously the monotypic *Kentrosiphon*. The cytology of the last mentioned species is unknown, and only their morphological features have been used to determine their relationships.

Morphology

In the five genera under discussion there is a trend towards an increasing modification of the flower. In the least modified genus, *Homoglossum*, the perianth segments can be subequal but there is a tendency for an increase in the size of the uppermost segments in some species. In this genus the most modified species appears to be *H. vandermerwei* where the upper segment is the longest, and the three lower very much smaller than the upper ones (fig. 24: G). All the

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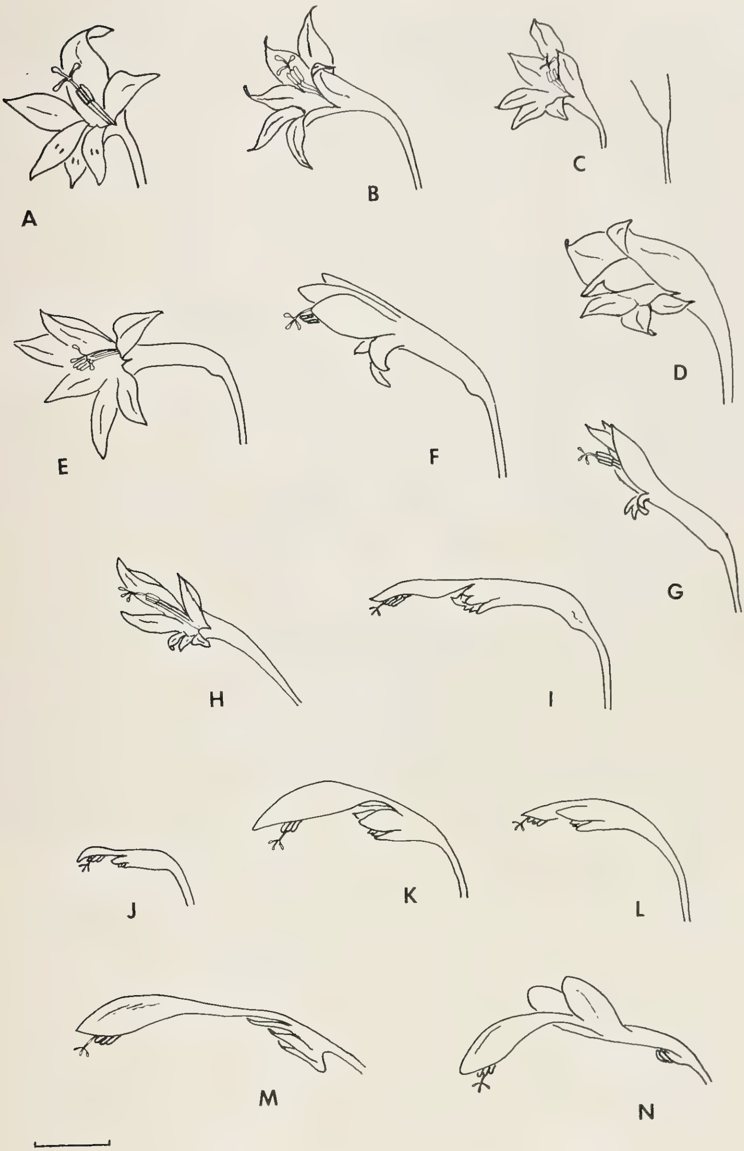
FIG. 24.

Flower structure in *Gladiolus* and its allies. A. *Gladiolus blandus;* B. *G. tristis;* C. *G. aureus;* D. *G. dracocephalus;* E. *Homoglossum watsonium;* F. *H. guthrei;* G. *H. vandermerwei;* H. *Gladiolus buckerveldii;* I. *Homoglossum abbreviatus;* J. *Oenostachys vaginifer;* K. *O. zambeziaca;* L. *O. dichroa;* M. *Anomalesia saccata* (*Kentrosiphon*); N. *A. cunonia.*


A
B
C
D
E
F
G
H
I
J
K
L
M
N
2 cm

species in this genus have a similar perianth tube, narrow at the base, widening abruptly into a wider tubular portion and usually bearing a small sac on the abaxial side of the tube at the point where the perianth tube narrows. This sac is unfortunately not well developed in some species, e.g. *H. priori*, making identification difficult. This type of perianth is not found in *Gladiolus* (fig. 24: A—C) for although *G. aureus* has a similar tube with a rather abrupt constriction, it has no sac, and the upper portion is not tubular but widens progressively. Thus *Homoglossum* can always be distinguished from *Gladiolus* on the morphology of the perianth tube, although the flower of some species can otherwise easily be confused with *Homoglossum*.

Homoglossum abbreviatus (*Petamenes*) has the same type of perianth tube as other species of *Homoglossum*, but here the upper perianth segment is far larger than the others (fig. 24: I) and constitutes the diagnostic feature for the genus.

The flower modification in this species is of the same nature as in *Homoglossum* and differs merely in degree, the uppermost perianth segment being well developed. This difference is clearly one of degree and this together with their very similar vegetative characters prompted Bolus (1933) to write that *Petamenes abbreviatus* barely escaped being placed in *Homoglossum*.

The vegetative features shared by *Homoglossum* and *P. abbreviatus* are a small corm and a single slender, linear leaf with pronounced margins. These vegetative features bear a strong resemblance to those found in many species of *Gladiolus*, amongst others *G. tristis* and *G. liliaceus*, which constitute a natural group within that genus. The other type of vegetative form found in *Gladiolus* species such as *G. natalensis* and *G. floribundus*, also indicative of a natural grouping, consists of a larger corm and several rather broad, ensiform leaves.

The other South African species of *Petamenes*, *P. buckerveldii* (now treated as *Gladiolus*) has this latter vegetative form and is rather different from *P. abbreviatus* in having a tapering perianth tube (fig. 24: I) which widens gradually and lacks the sac found in *P. abbreviatus*. The perianth segments are also less modified so that the upper segment is not much larger than the others. In fact, this type of perianth tube and flower are very similar to those found in some species of *Gladiolus*. Its vegetative features, which differ from *P. abbreviatus*, indicate that it is misplaced in its present genus and it has accordingly been transferred to *Gladiolus*, probably a far more natural position for this species where its only slightly modified flower would not be out of place.

The remaining species of *Petamenes* are found in tropical and southern Africa and appear to form a natural unit. Most species have a large corm and several relatively broad, ensiform leaves. The flowers have a long perianth tube which is narrow at the base and broadens to form a wide throat. The widening is not, however, abrupt and there is no sac as found in *Homoglossum* and

Petamenes abbreviatus. The upper perianth segment is much enlarged and hood-like, the two upper lateral segments are far smaller and the lower segments even smaller (fig. 24: K, L).

The two species of *Oenostachys* have a similar vegetative form and flower (fig. 24: L) and differ only in having unusually large bracts. *Oenostachys dichroa* is also reported to have bifid stigmas, but this feature is probably not significant in this case for, as the author has pointed out in a previous section, bifid stigmas occur randomly throughout the tribe *Ixieae* and probably do not have the taxonomic importance once accorded them. It is more likely that this plant has the usual bilobed stigmas of most species of *Gladiolus* and allies but with a more pronounced cleft.

Kentrosiphon and *Anomalesia* also have large corms and several fairly broad leaves but have the most modified flowers in the group (fig. 24: M, N). In both, the perianth tube is short and narrow and the uppermost segment is extremely large and hooded. The three lower segments are small and are bent upwards forming a sac-like structure. In *Anomalesia* the two upper lateral segments are large and form reflexed wings, while in *Kentrosiphon* these segments are smaller and form, with the lower segment, a part of the sac at the mouth of the perianth tube. In this genus the sac is more strongly developed and has a small spur extending backwards.

Taxonomic history

Many species in the five genera discussed in this section have at some period been regarded as allied to *Gladiolus*. The type species of *Petamenes* and of Homoglossum were originally described as species of *Gladiolus* and the type species of *Anomalesia* was at one time transferred to *Gladiolus*, having first been described as a species of *Antholyza*. Baker (1896) placed all the species of the group in *Antholyza*. In his expanded concept of this genus, Baker included not only the zygomorphic allies of *Gladiolus*, but species unrelated to these like *Antholyza ringens*, an ally of *Babiana*, and *Curtonus paniculatus*, regarded by the present author as a *Crocosmia*.

The basis for the genus *Antholyza* as understood by Baker was the medianly zygomorphic flower with a long perianth tube, this being peculiar in having a narrow basal portion which widened rather abruptly into a wide tubular upper part. Many of the species included in this group also had a rather large expanded upper perianth segment, often hood-like.

This unnatural assemblage was revised by N. E. Brown (1932) but prior to this the genus *Oenostachys* containing a single species with vegetative features and a flower exactly like the tropical African species of *Antholyza* was described by Bullock (1930). The species was not placed in *Antholyza* mainly because of its very large wine coloured bracts which completely enveloped the flowers and its bifid stigmas.

Brown continued the fragmentation of *Antholyza*, recognising *Oenostachys* and adding another species to this genus. Out of *Antholyza* (sensu Baker) Brown recognised ten genera; *Petamenes* and *Homoglossum* were revived, having originally been described by Salisbury; *Antholyza* was left as a monotypic genus; and six new genera were created. This treatment was more satisfactory than Baker's concept but proved a little unwieldy owing to the large number of genera that were recognised, many being monotypic or containing very few species. Brown's treatment has been altered slightly by later workers who sought to simplify it and to decrease the number of genera.

The first of these was Hutchinson (1934) who, in his classification of the Iridaceae, recognised the tribe *Antholyzeae* containing all but one of the genera originally placed in Baker's genus *Antholyza*, the exception being *Oenostachys* which was placed in the same tribe as *Gladiolus*. Hutchinson recognised all but one of Brown's genera, merging *Chasmanthe* and *Petamenes*. In view of the cytological evidence (see chapter on *Tritonia* and its allies) *Chasmanthe* having 20 somatic chromosomes and *Petamenes* 30, the value of this step must be regarded with doubt. The tribe *Antholyzeae* as constituted by Hutchinson is no more natural than Baker's genus, for it still contains disparate elements similar only in flower structure.

Phillips (1941) modified Brown's treatment further, as he incorporated *Anomalesia* and *Kentrosiphon* together with the probably unrelated *Chasmanthe* in *Petamenes*, a grouping he recognised as having the upper perianth segment large and hooded. Apart from the inclusion of species of *Chasmanthe*, Phillips' step has its merits for it reduced the number of genera and attempted to maintain the natural groupings. The modifications made by Hutchinson and Phillips were not followed by taxonomists and Lewis (1954) continued to recognise all of Brown's genera though she suggested the incorporation of *Kentrosiphon* in *Anomalesia*.

Lewis pointed out the diverse nature of the old genus *Antholyza* and grouped the genera created from it in more natural positions, placing, for example, *Chasmanthe* near *Crocosmia* and *Curtonus*, and *Antholyza* near *Babiana* (see relevant chapters). In doing so she placed less emphasis on floral morphology and took vegetative features into account. Lewis recognised two independent lines of evolution from *Gladiolus*, one leading to *Anomalesia* (including *Kentrosiphon*) and the other to *Homoglossum* and *Petamenes*. This treatment certainly seems the most natural, for though the floral modifications are similar, the first group has several broad leaves and the second only one or two linear leaves.

A proposed rearrangement of the genera

It is with some misgiving that the present author undertakes a re-evaluation of the status of this group of genera, once classified in the genus *Antholyza*.

That they do constitute a natural group is now quite clear for not only do they resemble different species of *Gladiolus* in their vegetative characteristics but appear from the evidence of breeding experiments and cytological study to form a potentially interfertile complex.

The close study of the kind of modification occurring in the flower together with the vegetative features indicates that there are two separate evolutionary lines and that in both a similar trend has occurred leading to increasingly zygomorphic flowers. All the genera are very closely allied to *Gladiolus*, and an argument can be made for their inclusion in that genus. This is particularly true of the less specialised species. As *Gladiolus* is itself a very large and already unwieldy genus of about 150 species this step would certainly not be advisable. It is thus proposed to treat the group in as natural a manner as possible and to arrange it in as convenient a system as can be devised. The question of convenience is an awkward one for it is difficult to know what will cause least difficulty. The following system is proposed.

Homoglossum

The genus *Homoglossum* is maintained and expanded to include *Petamenes abbreviatus* which is naturally allied to this genus. In its revised form *Homoglossum* now includes those plants with subequal or unequal perianth segments where the upper segment is enlarged to form a hood. In all species the perianth tube consists of a narrow basal and abruptly widened upper portion with a small sac at the junction of the wide and narrow parts. The vegetative form in this genus consists of a small corm and a few slender leaves, usually only one. As already pointed out, *Homoglossum* would be a genus of convenience, and should be recognised only if it continues to be such. The somewhat arbitrary difference between *Homoglossum* and *Gladiolus* may necessitate several changes in nomenclature later.

Oenostachys

As already mentioned, *Petamenes buckerveldii* does not really belong to the genus *Petamenes* and it has been transferred to *Gladiolus* where its only slightly modified flower is not unusual. The remaining species of *Petamenes* should be transferred to *Oenostachys*. The flower in these species is modified in the same way as in *Homoglossum* with a hood-like upper segment but has a perianth tube with a tapering upper portion and is without a sac. The vegetative form is similar in most species and consists of a large corm and several broad ensiform leaves. The major difference is in the size of the bracts which are largest in *O. dichroa*, smaller in *O. abbreviatus* which forms a link between *O. dichroa* and the remainder of the group which have smaller bracts.

Anomalesia

Finally, *Kentrosiphon* is incorporated in *Anomalesia*. The idea that these two genera should be combined is not new, for Klatt (1882) placed both in his new but nomenclaturally invalid genus *Anisanthus*. Lewis (1954) also suggested that they be merged. Although the flowers are rather different in appearance they are modified in a similar way. The perianth tube is narrow and short and the lower segments form a sac-like structure at the mouth of the tube. The vegetative features are similar and like most species in the previous group, the species have large corms and several relatively broad ensiform leaves.

Conclusion

The genus *Gladiolus* and its allies, however circumscribed, form one single group of genera sharing a number of morphological features, a similar karyotype and can in many instances be crossed. These genera should be placed in subtribe *Gladiolineae*. The genera recognised by the present author in this subtribe are *Gladiolus*, *Radinosiphon*, *Homoglosusm*, *Oenostachys* and *Anomalesia*.

f. Subtribe ***Ixiineae***

Dierama, Ixia, Sparaxis, Synnotia

This group comprises herbaceous plants with both evergreen and deciduous aerial leaves. All representatives have a corm, covered with reticulate fibres and in general have fairly unspecialised flowers, the exception being *Synnotia* where some species are very zygomorphic. The bracts are generally dry and membranous and the style branches short and undivided.

DIERAMA

$2n = 20$.

There are about twenty species in this genus, distributed along the mountainous regions of Africa from Ethiopia to the eastern Cape. The plants are comparatively large for the tribe *Ixieae* and are unusual in that many species are evergreen. *Dierama* is characterised by having a tall, branched scape with pendulous spikes of large actinomorphic, short-tubed flowers. A very characteristic feature of the genus is the large, dry, scarious bracts.

The five species examined here (Table 14) all have a similar karyotype in which the diploid number is 20 (fig. 25: A—E). The chromosomes range from 1,5 to about 3μ long. The larger ones are acrocentric and the smaller submetacentric. There are two pairs of chromosomes which are appreciably longer than the others and the second longest of these bears a satellite, though this is not always clearly seen. Occasionally a second satellite on a small chromosome is seen but as this is not clear it has not been included in the idiogram for *Dierama* based on the karyotype of *D. gracile*.

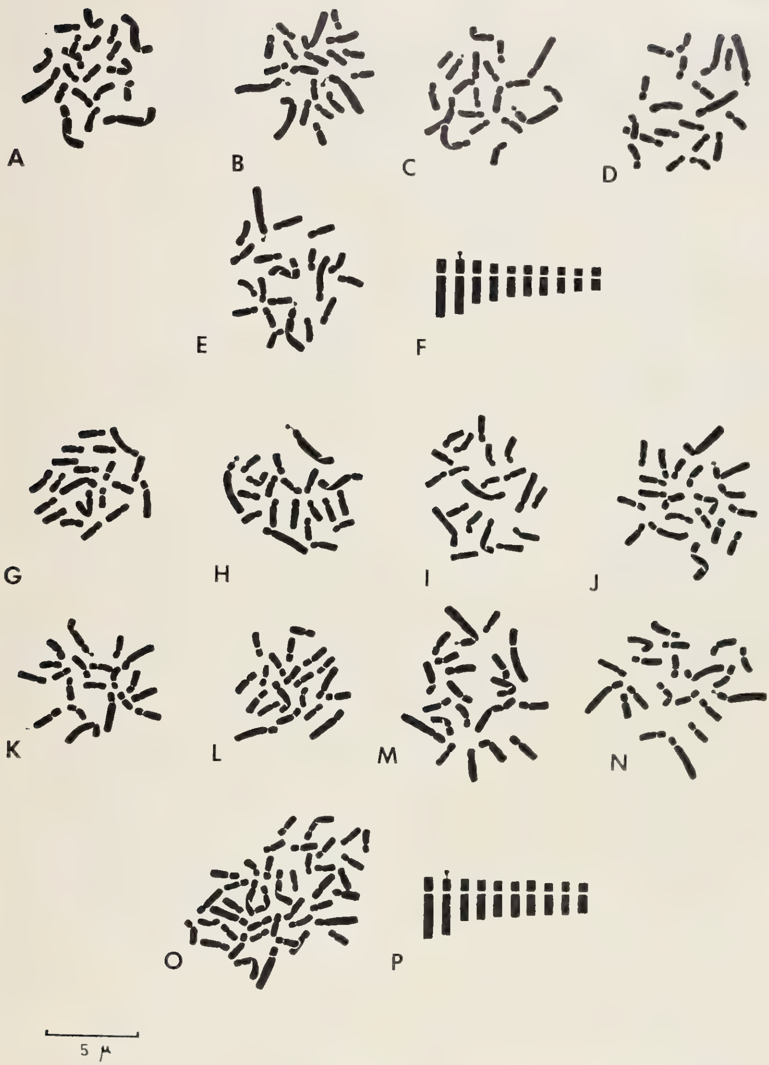


FIG. 25.

Karyotypes and idiograms of *Dierama* and *Ixia*. A. *Dierama galpinii;* B. *D. gracile;* C. *D. reynoldsii;* D. *D. medium aff.;* E. *D. luteo-albidum;* F. Idiogram of *Dierama;* G. *Ixia rapunculoides;* H. *I. odorata;* I. *I. longituba;* J. *I. erubescens;* K. *I. scillaris;* L. *I. flexuosa;* M. *I. dubia;* N. *I. polystachya;* O. *I. orientalis;* P. Idiogram of *Ixia*.

Only one species of Dierama has previously been studied cytologically, namely *D. pendulum* by Vilmorin & Simonet (1927) who found 2n = 20, a count confirmed by Goldblatt (1969). With a total of six of the twenty species in this genus having been reported as having a similar karyotype with a diploid number of 20, it is assumed that the basic number in the genus is 10.

TABLE 14
Chromosome numbers in *Dierama*, *Ixia*, *Sparaxis* and *Synnotia*.

Species	Diploid No.	Collection Data or Reference
DIERAMA C. Koch		
D. pendulum (L.f.) Koch	20	Vilmorin & Simonet 1921; Goldblatt 1969.
D. galpinii N.E. Br.	20	Saddleback, Barberton, Tvl. *Goldblatt 21* (J)
D. gracile N.E. Br.	20	Haenertsburg, Tvl. *Goldblatt 59* (J)
D. reynoldsii Verdoorn	20	Bergville, Natal. *Goldblatt 162* (J)
D. medium N.E. Br.	20	Wolkberg, Tvl. *Goldblatt 153* (J)
D. luteo-albidum Verdoorn	20	Lions River, Natal. *Davidson s.n.* (J)
IXIA L.		
I. campanulata Houtt. (as I. crateriodes)	20	(Brittingham 1934)
I. viridiflora Lam.	20	(Collins, fide Darlington & Wylie 1955)
	20	(Goldblatt 1969)
I. ranunculoides Delile	20	Nieuwoudtville, C.P. *Goldblatt 159* (J)
I. odorata Ker.	20	Malmesbury, C.P. *Goldblatt 505*
I. longituba N.E. Br.	20	Riversonderend, C.P. *Goldblatt 452*
I. erubescens Goldblatt (=I. crispa)	20	Tulbagh Road, C.P. *Goldblatt 202*
I. scillaris L.	20	Pakhuis Pass, C.P. *Goldblatt 104*
I. flexuosa L.	20	Quoin Point, C.P. *Goldblattt 332*
I. dubia Vent.	20	Kalk Bay Mountains, C.P. *Goldblatt 325*
I. polystachya L.	20	Table Mountain, Cape Town, C.P. *Goldblatt 377*
	20	(Fernandes & Neves 1961)
(as I. leucantha)	20	(Fernandes & Neves 1961)
I. orientalis L. Bol.	40	Hogsback, C.P. *Goldblatt 391*
SPARAXIS Ker		
S. tricolor (Schneev.) Ker	20	Nieuwoudtville, C.P. *Goldblatt 137* (J)
	20	(Brittingham 1934)
	20	(Nakajima, fide Darlington & Wylie 1955)
S. elegans (Sweet) Goldblatt	20	Nieuwoudtville, C.P. (Goldblatt 1969)
S. bulbifera (L.) Ker	20	Ysterplaat, Cape Town, C.P. *Goldblatt 262*
S. pillansii L. Bol.	20	Nieuwoudtville, C.P. *Goldblatt 327*
S. fragrans (Jacq.) Ker	20	Botrivier, C.P. *Goldblatt 296*
S. grandiflora subsp. fimbriata (Lam.) Goldblatt	20	Signal Hill, C.P. *Goldblatt 265*
subsp. acutiloba Goldblatt	20	Clanwilliam, C.P. (Goldblatt 1969)
SYNNOTIA Sweet		
S. villosa (Burm. f.) N.E. Br.	20	Hopefield, C.P. *Goldblatt*
S. galeata (Jacq.) Ker	20	Van Rhyns Pass, C.P. *Goldblatt*
S. variegata Sweet	20	Clanwilliam, C.P. (Goldblatt 1969)

All localities are in South Africa. The provinces are abbreviated as follows: Cape Province—C.P.; Transvaal—Tvl. Unless otherwise stated all specimens are housed at the Bolus Herbarium Cape Town.

IXIA

Ixia is believed to be a derivative of *Dierama* and is found mainly in the winter rainfall region of the Cape Province. The plants are smaller than *Dierama*, and the aerial parts are deciduous. The flowers are generally smaller, not pendulous, and have smaller membranous bracts.

There are forty-four species recognised in this genus, nine of which were examined here. In all but one, the diploid number is 20. The odd one, *Ixia orientalis* has $2n = 40$, and appears to be a polyploid species (fig. 25: G—P). The chromosomes range from 1,5 to 3,3μ and are acrocentric, though the smaller ones tend to be submetacentric. There are two pairs of longer chromosomes and the shorter of these bears a satellite. As the karyotypes of all the species examined are similar, the idiogram, based on *I. dubia* can be regarded as representative of the genus. A comparison of the idiograms of *Dierama* and *Ixia* shows the great similarity between these two genera.

Prior to this work, three named species of *Ixia* had been studied cytologically (Table 14), a diploid number of 20 being reported for all three. In addition, different hybrids studied by Brittingham were found to be diploid and polyploid, having somatic chromosome numbers of 20 or 40. Of the nine species studied in this work, eight are new chromosome counts and the record for *I. polystachya* confirms the previous count of Fernandes & Neves.

The karyotype as described by Brittingham and Fernandes & Neves confirms the finding by the present author that it consists of two long pairs and eight short pairs of chromosomes. With a total of eleven of the forty-four species in the genus having now been studied, it can be suggested that the basic number for the genus is 10.

The occurrence of polyploidy in *I. orientalis* is unusual, as polyploids are not common in South African Iridaceae, particularly in the tribe *Ixieae*, although polyploid species have been found in *Romulea*, *Geissorhiza*, *Tritonia* and *Gladiolus*. Before it can be decided that *I. orientalis* is a consistently polyploid species, other populations should perhaps be examined. It is, however, interesting to note that *I. orientalis* occurs in the easternmost limit of the range of distribution of the genus, and it is the only species of *Ixia* in the summer rainfall area.

The subgenus *Dichone*

The subgenus *Dichone* of *Ixia* is a group of species which was transferred by Lewis (1962) from *Tritonia* to *Ixia*. Although species placed in *Dichone* were originally referred to *Ixia* they were considered by Klatt (1882) and Baker (1876) to belong to *Tritonia*, and remained in that genus until transferred by Lewis, who did so on purely morphological grounds.

The two species in this group which were studied here, namely *I. scillaris* and *I. crispa* were found to have a diploid number of 20 and karyotypes similar to those of other species of Ixia. *Tritonia* and its allies, however, have a rather different karyotype and a basic number of 11. Thus cytological evidence confirms the decision of Lewis to transfer this group to *Ixia*.

The relationship between *Ixia* and *Dierama*

Ixia and *Dierama* have very similar karyotypes (fig. 25). This is evidence of the close relationship of the two genera, and confirms the accepted view that *Dierama* merges into *Ixia* and that *Dierama* gave rise to *Ixia*. It has been suggested by Lewis (1962) and supported by Goldblatt (1969) that *Dierama* which has a wide distribution from tropical Africa to the eastern Cape Province is the more primitive genus, while *Ixia* which is limited to the southern and western Cape Province is derived from it. The reasons proposed for this view are that *Dierama* has a series of unspecialised features, e.g. evergreen habit, much branched inflorescence, large persistent corms and regular flowers with a short perianth tube. It is believed that *Ixia* evolved from *Dierama* in response to the more exacting ecological conditions in the western Cape Province, for *Ixia* has deciduous aerial leaves, a small short-lived corm, a brief growing season and reduced inflorescence with more specialised flowers, all of which are believed better suited to the long, dry, hot summer, the wet winter and short spring period.

SPARAXIS

$2n = 20$.

Sparaxis is a small genus comprising six species, occurring in the south-western Cape Province. The plants are small with erect, usually unbranched inflorescences of large brightly coloured, regular or sub-zygomorphic flowers. A characteristic feature of the genus is the large, dry, scarious and lacerated bracts, similar to those in *Dierama*.

Five of the six species of *Sparaxis* were studied in the present work (Table 14). All exhibit a constant and characteristic karyotype. The diploid number is 20 and the chromosomes are fairly small and acrocentric (fig. 26: A—E). There appear to be two pairs of longer chromosomes one bearing a satellite. The size range is from about 1,5 to 3μ. Thus the karyotype is similar to that of *Ixia* and *Dierama*, though all the chromosomes tend to be slightly smaller. The idiogram of the karyotype of *S. grandiflora* (fig. 26: F) can be regarded as representative of the genus.

Prior to this work, three species of *Sparaxis* had been cytologically investigated, all having a diploid number of 20. In the present study the remaining three species were investigated for the first time while the counts for *S. tricolor* and *S. grandiflora* subsp. *fimbriata* confirm previous reports for these two.

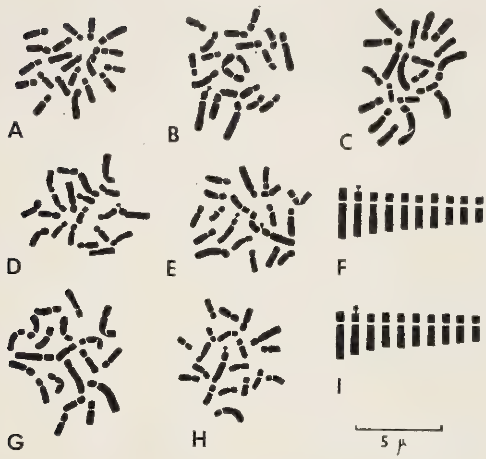


FIG. 26.

Karyotypes of *Sparaxis* and *Synnotia*. A. *Sparaxis tricolor;* B. *S. bulbifera;* C. *S. pillansii;* D. *S. fragrans;* E. *S. grandiflora* subsp. *fimbriata;* F. Idiogram of *Sparaxis;* G. *Synnotia villosa;* H. *S. galeata;* I. Idiogram of *Synnotia.*

As all the species in the genus have been studied it is clear that the basic number for the genus is 10. Brittingham (1934) and Goldblatt (1969) reported that the karyotypes of *Sparaxis* and *Ixia* are remarkably similar, an observation repeated in the present study, although the chromosomes of *Sparaxis* appear to be slightly smaller than those of *Ixia*. This similarity of karyotype may perhaps be regarded as evidence of phylogenetic relationship and will be discussed after the section on *Synnotia.*

SYNNOTIA

$2n = 20$.

Synnotia is another small genus occurring in the south western Cape. It is closely allied to *Sparaxis*, the plants differing only in having longer tubed, zygomorphic flowers.

Two of the five species in this small genus were examined cytologically (Table 14). The karyotypes of both are similar, and resemble *Sparaxis* closely. The diploid number is 20 and of the range of fairly small chromosomes, two pairs are conspicuous, being somewhat larger. The size of the chromosomes is the same as in *Sparaxis*. In only one of the longer chromosomes of *S. galeata*

a satellite was seen while none were visible in *S. villosa*. However, this satellite has been included in the idiogram of the karyotype of *S. galeata* as it is suspected that the satellites are present even if not often clearly seen (fig. 26: I).

The first cytological record for this genus was that of Goldblatt (1969) who obtained a diploid number of 20 in *S. variegata*. It was also reported that the karyotype closely resembled those of *Sparaxis*, *Dierama* and *Ixia*. Two more species have been examined in this work with similar results. The karyotype of *Synnotia* resembles most closely that of *Sparaxis* in that the chromosomes are slightly smaller than in *Ixia* and *Dierama* (fig. 26: G—I).

A suggested phylogeny of *Sparaxis* and *Synnotia*

That *Dierama*, *Ixia*, *Sparaxis* and *Synnotia* form a natural group was suggested by Goldblatt (1969). These genera all have a basic number of 10 and have a karyotype unique in the Iridaceae. The relationship between *Dierama* and *Ixia* has already been discussed and it is believed that *Sparaxis* and *Synnotia* were derived from *Dierama* in a way similar to that described for *Ixia*.

Both *Sparaxis* and *Synnotia* are deciduous and have a short growing season. They are small in size and are modified to resist very dry conditions. Both have, however, some features in which they resemble the genus *Dierama* very closely; the bracts and bracteoles of the three genera are unusual in the Iridaceae, being firm, dry, scarious and often lacerated; the capsules are comparatively hard walled and contain seeds which are unusual in that they are round and very glossy.

It is believed by the present author that *Synnotia* was derived from *Sparaxis*. They share a large number of morphological features, a similar karyotype and, except for their flowers, cannot be distinguished. These genera appear to be interfertile and a bigeneric hybrid between *Sparaxis* and *Synnotia* has been obtained. The capsules were fully developed and the seed was viable (Goldblatt 1969). Though the hybrids have not yet flowered they are growing vigorously.

The taxonomic position of *Synnotia*

The morphological differences between *Sparaxis* and *Synnotia* are slight for they differ only in flower structure. The flowers of *Sparaxis* are actinomorphic or sub-zygomorphic and have a very short perianth tube, while in *Synnotia* the flowers are highly zygomorphic and have a comparatively long and in some species, curved perianth tube. The perianth segments in *Sparaxis* are subequal but in *Synnotia* the posterior segment is somewhat enlarged and in most species forms a hood. Thus, the difference between the genera is in the degree of modification of their flowers.

This situation has a parallel in *Gladiolus* and its allied genera *Homoglossum*, *Petamenes* and *Anomalesia*, where again the degree of floral modification sepa-

rates the genera. It was suggested by the author that, for *Gladiolus* the unusual or extremely zygomorphic species be grouped in genera separate from *Gladiolus*, mainly for the sake of convenience. Although the degree of zygomorphy in *Synnotia* is perhaps not as extreme as in those genera allied to *Gladiolus*, it may be retained as a valid genus, again on grounds of convenience as well as minor morphological differences.

Intergeneric hybrids.

Apart from the already mentioned *Sparaxis x Synnotia* cross, no intergeneric hybrids were obtained in the four genera under discussion. The present author attempted crosses between *Dierama* and *Ixia* and between *Dierama* and *Sparaxis* (Table 1) but none was successful. This information can be taken as evidence that *Dierama*, *Ixia* and *Sparaxis* are quite distinct genera and if they are related, they have diverged sufficiently to exclude the possibility of any hybridisation taking place. As *Dierama* and *Ixia* are believed to merge into one another, more crosses should perhaps be attempted, particularly between the border-line species.

Conclusion

The relationship of the four genera, *Dierama*, *Ixia*, *Sparaxis* and *Synnotia* has often been regarded as fairly close and they have usually been placed in the same tribe or subtribe together with several other genera. Lewis (1954), who had a detailed knowledge of the South African Iridaceae, placed these four genera together with *Gladiolus* and its allies and *Tritonia* and allies in her subtribe *Ixiineae*. She states that attempts to divide the group into smaller units was difficult due to the great degree of morphological similarity. Hutchinson (1934) whose classification of the family was based mainly on flower structure, split the genera into tribes rather unnaturally resulting in *Dierama* and *Ixia* and *Streptanthera*, a genus incorporated in *Sparaxis* (Goldblatt 1969), being in a separate tribe from *Sparaxis* and *Synnotia*.

As has been shown in the present work the four genera under discussion share a number of morphological characteristics some of which are unique in the family, and appear to form a fairly natural group. These genera have been shown to have a similar and distinctive karyotype and have a basic chromosome number of 10 which confirms the evidence of morphological similarity. It is thus proposed that Lewis' subtribe *Ixiineae* be maintained, though in a modified form, to comprise only *Dierama*, *Ixia*, *Sparaxis* and *Synnotia*.

g. Subtribe ***Tritoniineae***

Crocosmia (including *Curtonus*), *Tritonia*, *Chasmanthe* and *Montbretiopsis*

This group of genera are generally small, herbaceous plants with spherical to flattened corms with tunics of fairly fine fibres. The slightly zygomorphic flowers are usually yellow or orange, although reds and pinks do occur.

CROCOSMIA

$2n = 22$.

This genus occurs in the summer rainfall area of south east Africa, usually in forested highland areas. The genus is distinguished by its squat capsule, each loculus containing only a few seeds. The monotypic genus *Curtonus* is treated here as part of *Crocosmia* and reasons for this are presented in the following text.

Five of the seven species in the genus and one hybrid were examined by the present author (Table 15). The diploid number is 22 in the representatives examined (fig. 27: A—G). The chromosomes are quite small, ranging from under 2 to just less than 3μ in length. Although there is a graduation in size, six pairs of somewhat longer chromosomes can be recognised and the karyotypes have no striking features. Satellites are seldom clearly seen though one or two are sometimes noticed on the longer chromosomes. Only in *C. aurea* were three seen. However, it is presumed that there are actually four satellites in the karyotype. Thus the idiogram of *C. aurea* is shown with two long chromosomes bearing satellites. One unusual feature noticed in *C. aurea*, *C. pottsii* and the hybrid is the presence of a single pair of metacentric chromosomes which serve to distinguish these species. In the remaining three species the preparations yielded rather smaller chromosomes and the metacentric chromosomes could not be recognised easily and are not drawn.

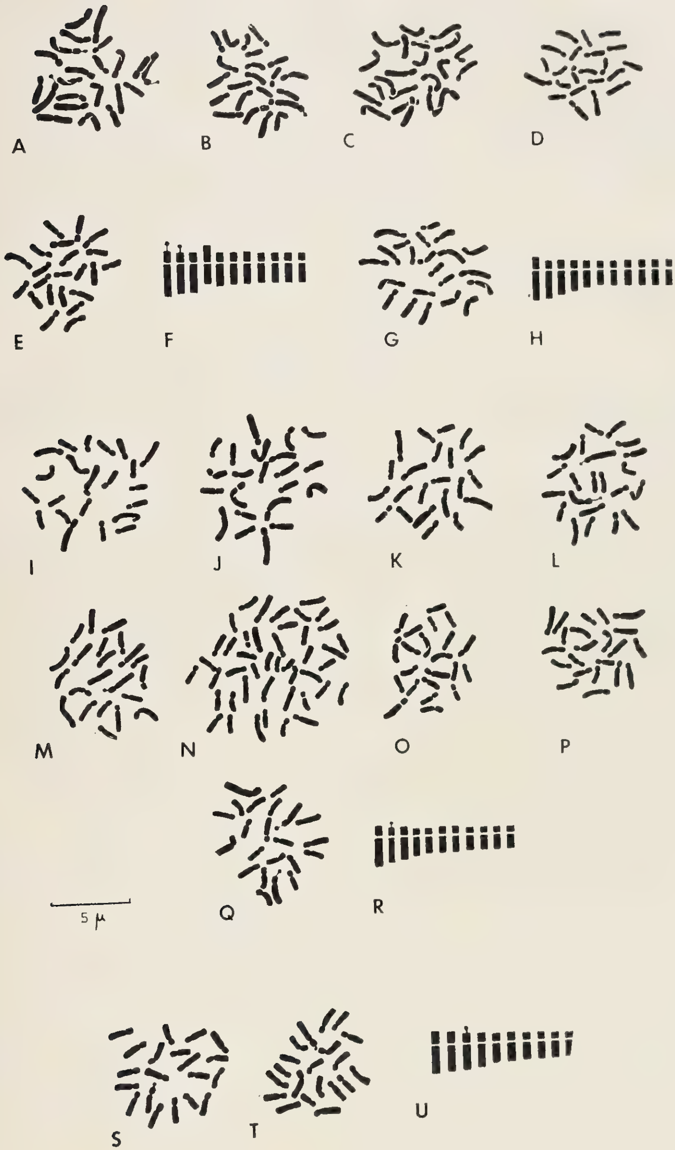
The present study confirms the previous counts for *C. aurea* and *C. pottsii* and also for the hybrid *C. x crocosmiiflora* (Table 15). In addition, *C. mathewsiana* and *C. masonorum* are reported here for the first time. As a diploid number of 22 has been recorded for the five species studied of the seven in the genus, it seems clear that the basic number in *Crocosmia* is 11.

Brittingham (1934) reported a chromosome number of 26 in *Antholyza paniculata*, a synonym of *Crocosmia paniculata*, studied here. There is little similarity between Brittingham's illustration and the karyotype described by the present author and it is suggested that Brittingham's count was not for this plant but some other species, the identity of which is unknown.

The plant known as *C. x crocosmiiflora* has long been regarded as a hybrid and it is, in fact, almost sterile for few seeds are ever produced. Both Ernst-Schwartzenbach (1930) and Brittingham (1934) postulated that it is a hybrid between *C. aurea* and *C. pottsii*. As far as the author is aware, this is only a suggestion and requires confirmation by actually repeating this cross.

FIG. 27.

Karyotypes and idiograms of *Crocosmia*, *Curtonus*, *Tritonia* and *Chasmanthe*. A. *Crocosmia aurea;* B. *C. pottsii*, C. *C. crocosmiiflora*, D. *C. masonorum*, E. *C. mathewsiana*, F. Idiogram of *C. durea;* G. *Crocosmia paniculata* (previously *Curtonus*); H. Idiogram of *C. paniculata;* I. *Tritonia moggii;* J. *T. coccinea;* K. *T. wilsonii;* L. *T. crispa;* M. *T. nelsonii;* N. *T. lineata;* O. *T. flabellifolia;* P. *T. deusta;* Q. *T. squalida;* R. Idiogram of *Tritonia;* S. *Chasmanthe aethiopica;* T. *C. floribunda;* U. Idiogram of *Chasmanthe*.


A
B
C
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E
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G
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L
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TABLE 15
Chromosome numbers in *Crocosmia*, *Tritonia* and *Chasmanthe*.

Species	Diploid No.	Collection Data or Reference
CROCOSMIA Planch		
C. aurea Planch	22	(Shibata, fide Index of Plants Chromosome Numbers, 1963)
	22	Woodbush, Haenertsburg, Tvl. *Goldblatt 11* (J)
C. pottsii (Bak.) N.E. Br. . .	22	(Ernst-Schwartzenbach 1930)
	22	(Nakajima, fide Darlington & Wylie 1955)
	22	Mooi River, Natal. *Goldblatt 98* (KJ)
C. × crocomiiflora (Nicholson) N.E. Br.	22	(Ernst-Schwartzenbach 1930)
	22	Brittingham 1934
	22	(Meurman & Suomalainen, fide Darlington and Wylie 1955)
	22	ex hort. *Goldblatt 516.*
C. masonorum (L. Bol.) N.E. Br.	22	ex hort. *Goldblatt 77* (J)
C. mathewsiana L. Bol. . . .	22	Graskop, Tvl. *Goldblatt 417*
C. paniculata (Klatt) Goldblatt .	22	Saddleback, Barberton, Tvl. *Goldblatt 61* (J)
(as Antholyza paniculata) . .	26	(Brittingham 1934)
TRITONIA Ker		
T. crocata (L.) Ker	20	(Brittingham 1934)
	22, 60.	(Sharma and Sharma 1960)
T. deusta (Ait.) Ker	22	Stormsvlei, C.P. *Goldblatt 514*
T. squalida (Ait.) Ker . . .	22	C.P. (ex hort) *Goldblatt 32* (J)
T. moggii Oberm.	22	Inhaca Island, Mozambique. *Goldblatt 2* (J)
T. coccinea L. Bol.	22	Port St. John, C.P. *Goldblatt 382*
T. wilsonii Bak.	22	Fort Hare, C.P. *Goldblatt 406.*
T. crispa (L.f.) Ker	22	Giftberg, C.P. *Goldblatt 436*
T. nelsonii Bak.	22	Linksfield Ridge, Johannesburg, Tvl. *Goldblatt 5.*
T. lineata (Salisb.) Ker . . .	42	Alice, Eastern C.P. *Goldblatt 438*
T. flabellifolia (de la Roche) Lewis	22	McGregor, C.P. *Lewis 6203* (NBG)
CHASMANTHE N.E. Br.		
C. aethiopica (L)N.E. Br. . .	32	(Nakajima, fide Darlington & Wylie 1955)
	20	Kirstenbosch, C.P. *Goldblatt 90* (J)
C. floribunda (Salisb.) N.E. Br. .	20	ex hort. *Goldblatt 467*

All localities given are in South Africa unless otherwise stated. The provinces are abbreviated as follows: Cape Province—C.P.; Transvaal—Tvl. Specimens are located at the Bolus Herbarium, Cape Town, unless stated to the contrary.

The taxonomic position of *Crocosmia paniculata*, previously regarded as a species of the genus *Curtonus*

Crocosmia paniculata, previously the only species in the monotypic genus *Curtonus*, is a tall, much branched plant with a bright orange, usually long-tubed zygomorphic flower. It occurs in the mountains of the eastern Transvaal and Natal. The diploid number of 22 and karyotype comprising small acrocentric chromosomes point to a relationship with species of *Crocosmia*, particularly *C. masonorum* and *C. mathewsiana* (fig. 27: G).

The similarity of the karyotype of *Curtonus* with its basic number of 11 to that of *Crocosmia* is not altogether rurprising, as *Curtonus* was regarded by Lewis (1954) as being intermediate between *Crocosmia* and the more specialised genus *Chasmanthe*. This similarity of karyotype must be regarded as confirmation of Lewis' suggestion on the affinity of *Curtonus*, although earlier workers separated it from *Crocosmia*.

Crocosmia paniculata was originally described as *Antholyza paniculata* by Klatt (1868) and was treated as such by Baker (1896). When *Antholyza* was revised by Brown (1932) he created the new genus *Curtonus* for this species. Hutchinson (1934) placed *Curtonus* in his tribe *Antholyzeae* which contained all the genera which Brown created out of *Antholyza*. The tribe *Antholyzeae* was thus as unnatural as the genus *Antholyza*. This classification left *Curtonus* and *Crocosmia* in different tribes until Lewis resolved the inconsistency.

Crocosmia paniculata is a fairly large plant regarded as unusual, as it has a stout stem with a slightly flexuose axis bearing many branches. The flower is also unusual for it has a somewhat curved perianth tube with a very narrow basal part and a hooded upper perianth segment.

A close examination of other species of *Crocosmia* reveals that all of these features occur in this genus: *C. aurea* and *C. mathewsiana* have a similar slightly flexuose stem with many branches; both *C. pottsii* and *C. mathewsiana* have a curved perianth tube; the upper segment in *C. mathewsiana* is slightly hooded. Thus it can be seen that *Curtonus* was a genus based on very inadequate grounds. The only unusual feature in *Curtonus* is the length of the perianth tube which is far longer than in any other species of *Crocosmia*. Thus it is proposed that *Curtonus paniculatus* should be regarded merely as a long-tubed species of *Crocosmia*. The necessary taxonomic corrections are made in a separate chapter.

TRITONIA

$2n = 22, 44.$

Tritonia is a large genus of about forty species which occurs throughout southern Africa. The plants are generally smaller in size than species of *Crocosmia*, are less branched and are distinguished from that genus by an elongated capsule containing many small seeds.

Nine species of *Tritonia* were examined and, as observed in *Crocosmia*, the karyotype is undistinguished. With the exception of *T. lineata*, all species have a diploid number of 22 (Table 15) and the chromosomes are fairly small ranging from 1,5 to 2,5μ. *T. lineata* has 44 chromosomes and must be regarded as a polyploid species. Several different populations of this species were examined and all have proved to be polyploid. The karyotypes of all the species are similar and the idiogram of *T. squalida* is represented here as characteristic

of the genus (fig. 27: I—R). Although the chromosomes vary rather little in length, three pairs of longer chromosomes can be distinguished. Satellites are not always seen, but when visible, as in *T. squalida*, they are located on the longer chromosomes. A metacentric chromosome is not present but the karyotype bears unmistakable resemblance to that of *Crocosmia*.

Only one species of *Tritonia* has previously been studied. Brittingham (1934) found 2n = 20 for *T. crocata* while Sharma & Sharma (1960) recorded 2n = 60 and 22 in cultivated varieties of the same species. In the light of the present work where nine more species were studied, all having a basic number of 11, it seems that only the one record of Sharma & Sharma is correct. Brittingham may have overlooked a pair of chromosomes or he may have been dealing with some other plant.

One of the nine species studied here, *T. lineata*, proved to be polyploid. No meiotic examination was made, but the species is fertile and breeds true. This is one of the few polyploid species in the tribe *Ixieae* and again, as in *Ixia orientalis* the polyploid species of *Gladiolus*, it is significant to note that it occurs in the summer rainfall area.

CHASMANTHE

2n = 20.

Chasmanthe is a small genus occurring in the southern and western Cape Province. The plant is characterised by its very zygomorphic flower with a long perianth tube and a large, hooded upper perianth segment. Only two of the ten recognised species were studied. Both have a diploid number of 20 and the chromosomes are all comparatively small and acrocentric (fig. 27: S—T). In size the chromosomes range from 1,5 to 2,5μ and of these, four pairs appear somewhat larger in size. In both species a satellite was observed on one of the large chromosomes. The idiogram of *C. floribunda* is illustrated as representative of the genus (fig. 27: U).

Prior to this work there has been one cytological report in this genus. Nakajima (fide Darlington & Wylie 1955) reported 2n = 32 for *C. aethiopica*. In the light of the present results of 2n = 20 for *C. aethiopica* and *C. floribunda* it would appear that the plant studied by Nakajima belonged to another genus. It may have been a species of *Tritoniopsis* or *Anapalina* which have diploid numbers of 32 and 34, and which resemble *Chasmanthe* to some extent.

The two cytological reports for *Chasmanthe* in the present work can be regarded as new records and it is tentatively suggested that the basic number for the genus is 10.

The genus *Montbretiopsis*

Montbretiopsis florentiae, the only representative of this rare genus is a small plant in which the aerial part of the stem has been reduced and the flowers

have a long perianth tube. Several attempts to collect this plant in the arid areas where it occurs were unsuccessful. Presumably the plant only flowers in seasons when the irregular rainfall has been sufficient. It was suggested by Lewis (1954) that the plant is allied to *Tritonia* and may even belong in this genus. It is hoped that a cytological examination will one day confirm or refute this view.

Possible phylogeny and evolution and the taxonomic affinity of *Chasmanthe*

It is clear from the similarity of the basic chromosome number and karyotype that *Tritonia* and *Crocosmia* are related. This is recognised by most authors, for these two genera are always placed next to one another in any treatment. The genera are so similar that there exists, even today, some confusion as to which species belong to which genus. N. E. Brown (1932) attempted to clarify the position by redefining both genera. Although several species have been described since, our knowledge is not yet complete enough to make it possible to decide whether *Crocosmia* is a valid genus or not. It seems that Brown's interpretation of the genera is essentially correct though it needs some modification. For the sake of convenience at least, the genus *Crocosmia* should be maintained.

The genus *Chasmanthe* was referred to *Petamenes* by Hutchinson (1934) and it was merged with *Anomalesia* and *Kentrosiphon* in *Petamenes* by Phillips (1941).

Chasmanthe does indeed resemble *Petamenes* in general floral structure for it has a similar long perianth tube with a slender basal and broad upper portion. The upper perianth segment is also very long and hooded as in *Petamenes*. The resemblance ceases here for the style and stigmas are different and the seeds are not winged as they are in *Petamenes*. The bracts resemble those of Tritonia while the large capsule containing few seeds and the corms are like those of *Crocosmia* and perhaps *Curtonus*.

Lewis (1954) regarded *Chasmanthe* as being most closely allied to *Crocosmia* and *Curtonus*. She considered *Chasmanthe* as the most specialised and advanced of the evolutionary line beginning with *Tritonia* and *Crocosmia*. The karyological evidence supports her interpretation more strongly than any other, for although the karyotype resembles that of *Tritonia* and *Crocosmia* in general size and appearance of the chromosomes, the basic number is 10, compared to 11 in *Tritonia* and *Crocosmia*. If Lewis' interpretation is correct, *Chasmanthe* has probably evolved from a *Crocosmia*-like ancestor, possibly *C. paniculata* by modification of the floral parts. During this process aneuploid reduction could also have occurred to produce the karyotype of *Chasmanthe*.

Cytological examination has confirmed the close relationship of *Tritonia* and *Crocosmia* (and *Curtonus*) and suggests the possible relationship of *Chasmanthe*.

It is suggested that these genera, together with *Montbretiopsis*, all of which seem to belong to a single phylogenetic line, be grouped in a new subtribe called *Tritonineae*. Previously these genera were placed in the *Ixiineae* of Lewis (1954) but as has been shown, cytological results reveal the presence of several lines within her subtribe (note the section on *Dierama* and allies).

Evolution in this group parallels that in *Dierama*. Species of *Crocosmia*, which are large plants occurring in the eastern mountains of southern Africa, appear to have given rise to *Tritonia* which is generally much smaller and occurs mainly in the winter rainfall area. Species of *Tritonia* appear to be more specialised and to grow in more arid conditions. *Chasmanthe* seems to be the most modified of all and it occurs in the winter rainfall area in the western Cape Province.

h. Subtribe ***Babianineae***

Babiana and *Antholyza* (including *Anaclanthe*)

This group comprises fairly small plants which have a very characteristic appearance: the leaves are pleated; the corms deep seated and covered by particularly tough tunics; pubescence occurs on all or some of the aerial organs.

BABIANA

$2n = 14.$

This is a large genus comprising about sixty species. It is found mainly in the winter rainfall area of the Cape Province, but representatives occur in the summer rainfall area of southern Africa and on the island of Socotra. The genus is fairly variable, both actinomorphic and zygomorphic species occur, though the degree of zygomorphy is less pronounced than in the other genera in this group.

Eleven species were examined by the present author and were found to have a diploid number of 14. Two exceptions were found, namely *B. sambucina* and *B. hypogea*, where supernumerary chromosomes were sometimes found in populations of these species. These will be discussed below.

The karyotypes of all the species of *Babiana* examined are similar (fig. 28: A—J). The centromeres are all sub-terminal, thus the chromosomes can be described as acrocentric, and the range in size is from 1,5 to just less than 5μ. There are two pairs of long chromosomes, the one pair being about $4{,}5\mu$ long and the shorter measuring 3,5 to 4μ. This shorter one possesses a satellite. The remaining five pairs range from under 3 to $1{,}5\mu$, and the second in length of

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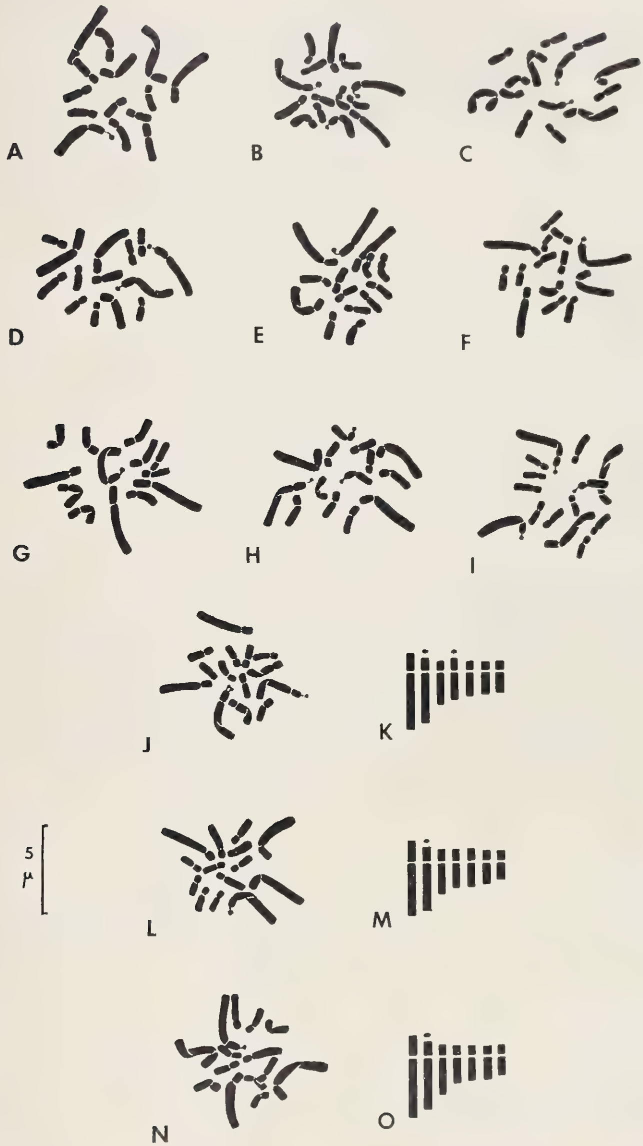
FIG. 28.

Karyotypes of *Babiana* and *Antholyza* (including *Anaclanthe*). A. *Babiana villosula;* B. *B. nana;* C. *B. scabrifolia;* D. *B. flabellifolia;* E. *B. vanzyliae;* F. *B. pubescens;* G. *B. sambucina;* H. *B. stricta;* I. *B. tubulosa;* J. *B. mucronuta;* K. Idiogram of *Babiana;* L. *Antholyza plicata* = *Anaclanthe*); M. Idiogram of *A. plicata;* N. *Antholyza ringens;* O. Idiogram of *A. ringens.*


A
B
C
D
E
F
G
H
I
J
K
5 μ
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M
N
O

TABLE 16

Chromosome numbers in *Babiana* and *Antholyza*.

Species	Diploid No.	Collection Data or Reference
BABIANA Ker		
B. disticha Ker	14	(Fernandes & Neves 1961)
B. flabellifolia Harv. ex Klatt	14	Calvinia, C.P. *Goldblatt 244*
B. hypogea Burch.	14+1–3B	Johannesburg, Tvl. *Goldblatt 16* (J)
	14	Witbank, Tvl. *Makunga* (Fort Hare)
	14 + B	Blyde Canyon, Tvl. *Davidson sn.* (J)
(as B. bainesii)	14	(Riley 1962)
B. mucronata (Jacq.) Ker	14	Citrusdal, C.P. *Goldblatt 248*
B. nana (Andr.) Spreng.	14	Darling, C.P. *Goldblatt 197*
B. pubescens (Lam) Lewis	14	Namaqualand, C.P. *Goldblatt 18* (J)
B. pulchra (Salisb.) Lewis (as B. atrocyanea)	14	(Zucconi 1956)
B. purpurea (Jacq.) Ker	14	(Zucconi 1956)
B. pygmaea (Burm. f.) N.E. Br. (as B. macrantha)	14	(Zucconi 1956)
B. rubrocyanea (Jacq.) Ker (as B. stricta v. rubrocyanea)	14	(Zucconi 1956)
B. sambucina (Jacq.) Ker	14 (+1–2B)	Clanwilliam, C.P. *Goldblatt 19* (J)
	14	(Zucconi 1956)
B. scabrifolia Brehm ex. Klatt	14	(ex hort) *Goldblatt 97* (J)
B. stricta (Art) Ker	14	Llandudno, C.P. *Goldblatt 43* (J)
	12	(Brittingham 1934)
	14	(Sugiura, fide Darlington & Wylie 1955)
	14+B	(Zucconi 1956)
B. stricta var. erectifolia Lewis (as B. erectifolia)	14	(Gwynn 1958)
B. stricta var. sulphurea (Jacq.) Bak. (as B. sulphurea)	14	(Sharma & Sharma 1960)
B. tubulosa (Burm. f.) Ker		Springbok, C.P. (ex hort) *Goldblatt 512*
B. tubulosa var. tubiflora (L.f.) Lewis (as B. tubiflora)	14	(Zucconi 1956)
	14	(Gwynn 1958)
B. vanzyliae L. Bol.	14	Nieuwoudtville, C.P. *Goldblatt 103* (J)
B. villosula (Gmel) Ker ex Steud		Oudekraal, C.P. *Goldblatt 89* (J)
B. villosa (Ait.) Ker	14	Oudekraal, C.P.
B. atrocyanea (an unknown species)	14	Zucconi (1956)
ANTHOLYZA L.		
A. ringens L.	14	Fish Hoek, C.P. *Goldblatt 83* (J)
A. plicata L.f.	14	Lamberts Bay, C.P. *Goldblatt 113* (J)

All localities are in South Africa and the provinces are abbreviated as follows: Cape Province—C.P.; Transvaal—Tvl. Specimens are located at the Bolus Herbarium, Cape Town, unless stated to the contrary.

these 5 pairs can sometimes be seen to bear a satellite. This character was noted in only four of the eleven species examined and thus does not seem to be a constant feature. However, it was probably overlooked in the other species, as satellites are not always clearly visible and often only one of a pair of satellities is seen.

As the karyotypes of the species vary only very little, a generic karyotype can be constructed. Here the idiogram of the karyotype of *B. stricta* is shown as representative of the genus (fig. 28: K). Other species do differ but the variation is minimal. Small size differences occur and there are slight changes in the position of the centromere and, as mentioned, the second satellite is not always seen. The variation is not significant for this study though it may be useful in a critical evaluation of *Babiana* alone.

The supernumerary of B chromosomes in *Babiana*

The variation in chromosome number in *B. sambucina* and *B. hypogea* follows a pattern found in several groups of plants. The extra chromosomes vary in number; even in the same root tip one, two or none can be found (fig. 29). This is typical of the behaviour of the so called B chromosomes. The reason is that these chromosomes frequently lag behind at anaphase.

Three populations of *B. hypogea* were examined. One from Witbank, Transvaal, had no B chromosomes. Populations from the eastern Transvaal escarpment, near Blyde River Canyon, had one or no extra chromosomes, while a population from Melville, Johannesburg, had one, two, three and sometimes even four. The significance of the B chromosomes is unknown and their occurrence does not seem to be correlated with morphological differences or climatic conditions.

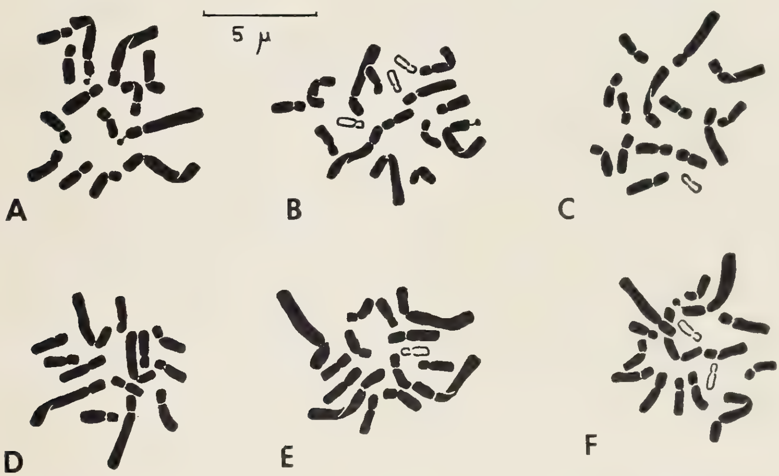

Fig. 29.

B chromosomes in *Babiana*. A – C metaphase plates of plants from a single population of *B. sambucina* showing none to three B chromosomes; D – F metaphase plates of plants from three different populations of *B. hypogea*, from Witbank, Transvaal; Blyde Canyon, Transvaal, and Johannesburg respectively.

The cytology of *Babiana* has been studied quite extensively. It is clear from the existing work that the diploid number is 14 for all species so far examined (Table 16). Of the eleven species studied by the present author, seven of the chromosome counts are new records and the remaining four, for *B. stricta*, *B. tubulosa*, *B. sambucina* and *B. hypogea* confirm the earlier reports. The occurrence of B chromosomes in *Babiana* was first recorded by Zucconi for *B. stricta*. These supernumerary chromosomes were again found by the present author in some populations of *B. hypogea* and *B. sambucina*. Although their significance is not known they play no part in phylogenetic considerations and thus are unimportant in the present study.

Thus, the total of seventeen species (plus one of unknown identity, *B. atrocyanea*) has been examined. Where the studies of earlier workers were sufficiently detailed, it can be seen that the karyotype for the genus as described in this work, confirms their results. The only conflicting report is that of Brittingham (1934) who found a diploid number of 12 in *B. stricta*. Since this species has been found by other workers to have a diploid number of 14, it seems that Brittingham's count was erroneous. A close examination of his illustration shows a pair of very long chromosomes with a median constriction. As this type of chromosome has not otherwise been recorded in *Babiana*, it is likely that this in fact represents two short chromosomes lying close together.

Babiana consists of sixty species thus it can be seen that a fair proportion of the genus has been studied. As there is no variation (apart from the report of Brittingham) it seems that a basic number of 7 for the genus can confidently be proposed.

ANTHOLYZA (including *Anaclanthe*)

$2n = 14.$

Antholyza, as treated here, is a small genus of two or perhaps three species occurring only in the western Cape Province. The flowers are modified, having a long upper segment sheathing the stamens and style, and reduced lower segments. The diploid number is 14 and as in *Babiana* the karyotype consists of 2 pairs of long chromosomes and 5 pairs of shorter ones. Satellites were observed on the second longest pair only. The karyotypes of *A. ringens* and *A. plicata* (previously *Anaclanthe*) are very similar and fit within the pattern observed for *Babiana*. The karyotype of this genus is described here for the first time. As can be seen from fig. 28, the karyotypes are very similar to those of *Babiana*.

Discussion

The morphological similarities between *Babiana*, *Anaclanthe* and *Antholyza* are striking; all have plicate leaves, a feature not common in the Iridaceae; some degree of pubescence, particularly on the stem and bracts, is present; the

corm is unique in the family, having peculiar tough papery tunics which extend upwards in a neck around the base of the stem; and the firm green bracts have brown tips. The difference between the genera is in the structure of the flower which is increasingly specialised and zygomorphic in *Anaclanthe* and *Antholyza* (fig. 30). In *Babiana* the flower structure ranges from actinomorphic to slightly zygomorphic. Species with the latter type of flower have a straight perianth tube slightly expanded at the throat. The posterior or upper perianth segment is somewhat larger than the others and widely separated from them, forming a slight hood. The upper lateral segments are partly united with the three lower segments, the latter forming a lip (fig. 30: A, B).

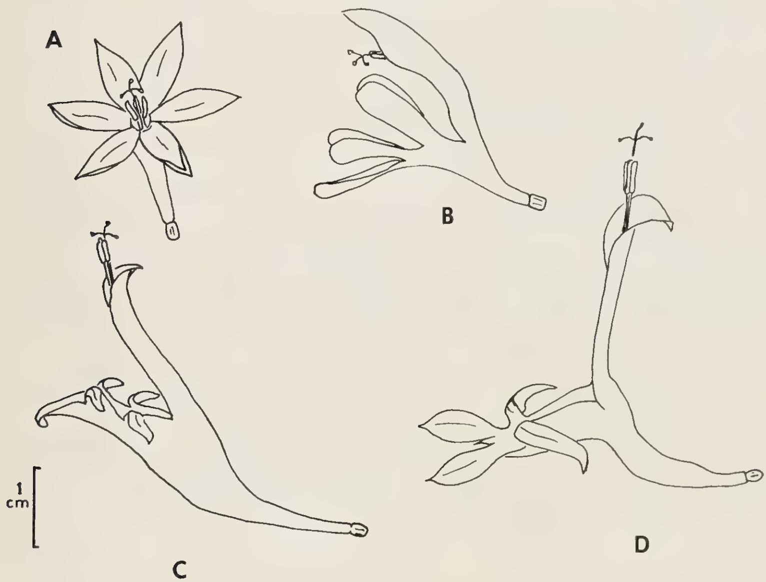

Fig. 30.
Flower structure in *Babiana* and its allies. A. *Babiana stricta;* B. *B. fimbriata;* C. *Antholyza plicata* (*Anaclanthe*)*;* D. *Antholyza ringens.*

This type of flower is rather different from that found in *Antholyza* and is extremely modified (fig. 30: C, D). The perianth tube is long and bent upwards. The hood-like posterior segment is much larger than the other segments and envelops the lower part of the stamens and style. The other segments are partly united with the three lower ones forming a lip. The same type of flower occurs both in *A. plicata* and *A. ringens*, but in the latter the zygomorphic

trend is accentuated (fig. 30: D). The upper segment is larger than in *A. plicata* and is more widely separated from the other segments which are united for most of their length. The upper lateral segments are reflexed while the lower lateral segments form a large lip and the lower segment is much reduced. In *A. ringens* the inflorescence is also modified in that the main stalk is sterile and stands erect bearing a few bracts only, while a lower branch bears the flowers.

Thus, while the distinct flowers of *Anaclanthe* and *Antholyza* have served as the basis for the recognition of these two genera, they have tended to disguise their correct relationships. The difficulty is paralleled in the relationship between *Gladiolus* and *Crocosmia* and their respective more zygomorphic allies. The problem has been resolved in the same way by reducing the number of genera with zygomorphic flowers. These genera are often very small but should be maintained as distinct from the presumed parent genus both for convenience and in recognition of their very specialised flower. Accordingly, *Anaclanthe* has been included in *Antholyza* by the present author.

Taxonomic History

The genus *Antholyza* has had a very confused taxonomic history. The relationship between the type species, *A. ringens* and *Babiana* has often been misunderstood and these two obviously allied genera have at times been placed in different tribes. The second species of *Antholyza* studied here, *A. plicata*, has been transferred by the present author from *Anaclanthe* back to *Antholyza*. This species was in fact referred to *Antholyza* when first described by the younger Linnaeus, but was subsequently treated as a *Babiana* by most authors.

Diels (1930) recognised the similarities between *Babiana*, *Antholyza* and species previously referred to as *Anaclanthe*. He placed the species of the latter two genera in a separate section of *Babiana*. Diels upheld the genus *Antholyza* although without the type species *A. ringens* this was taxonomically invalid. When Brown (1932) revised the genus *Antholyza* (sensu Baker), he ignored Diel's view. Instead he recognised *Antholyza ringens* as the only species in this genus and created the new genus *Anaclanthe* for *A. ringens*. Hutchinson (1934) followed Brown's treatment and placed *Anaclanthe* and *Antholyza* in the tribe *Antholyzeae* with the other members of Baker's *Antholyza*, while referring *Babiana* to a separate tribe. Lewis (1954) recognised the true affinities of the three genera and placed them in her subtribe *Babianineae*. Her treatment, which takes into account all morphological features, results in a more natural classification which is confirmed by cytological evidence.

As *Antholyza* and *Anaclanthe* are morphologically so similar to *Babiana* and share a common karyotype unique in the family, Lewis' subtribe *Babianineae* has been maintained. *Anaclanthe* has now been incorporated in *Antholyza* so that this subtribe comprises only two genera, *Babiana* and *Antholyza*, the latter distinguished from Babiana by its very specialised flowers.

i. Subtribe ***Exohebeineae***

Tritoniopsis and *Anapalina*

This subtribe consists of a pair of closely related genera, occurring in the mountains of the winter rainfall area of the Cape Province. The plants are typically summer flowering, when the spicate inflorescences of colourful flowers are often conspicuous. *Tritoniopsis* is the less modified, having actinomorphic to slightly zygomorphic flowers with a short perianth tube, while *Anapalina* has a long tube and a large hooded upper perianth segment.

TABLE 17
Chromosome numbers in *Tritoniopsis* and *Anapalina*.

Species	Diploid No.	Collection Data or Reference
TRITONIOPSIS L. Bol		
T. leslei L. Bol.	32	Cascades, Ceres, C.P. *Goldblatt 409*
T. lata (L. Bol.) Lewis . . .	32	Betty's Bay, C.P. *Goldblatt 186*
T. parviflora (Jacq.) Lewis . .	32	Silvermine Plateau, C.P. *Goldblatt 410*
T. unguicularis (Lam.) Lewis .	32	Silvermine Plateau, C.P. *Goldblatt 411*
ANAPALINA N.E. Br.		
A. nervosa (Thunb.) Lewis . .	34	Nieuwoudtville, C.P. *Goldblatt 286*
A. triticea (Burm. f.) N.E. Br. .	34	Constantia Nek, C.P. *Goldblatt 403.*

All specimens were collected in the Cape Province, South Africa, and are housed at the Bolus Herbarium, Cape Town.

TRITONIOPSIS

2n = 32.

The genus *Tritoniopsis* comprises fourteen species. Four species were examined in this study and all were found to have a diploid number of 32 (Table 17). As can be seen from fig. 31: A—D, the karyotypes have no remarkable features. All the chromosomes are acrocentric and uniformly small, ranging from 1 to 1,5μ in length.

ANAPALINA

2n = 34.

Two of the seven species in this small genus were studied (Table 17). In both the diploid number was found to be 34. The karyotypes comprise small acrocentric chromosomes ranging in length from 1 to 1,5μ (fig. 31: E, F).

The affinities of *Tritoniopsis* and *Anapalina*

These two genera are closely allied and form a natural group. They are unique in the Iridaceae in posessing the following series of characteristics: coriaceous leaves bearing several distinct main veins; dry, firm bracts and bracteoles of which the latter are longer, inflated capsules bearing light seeds with

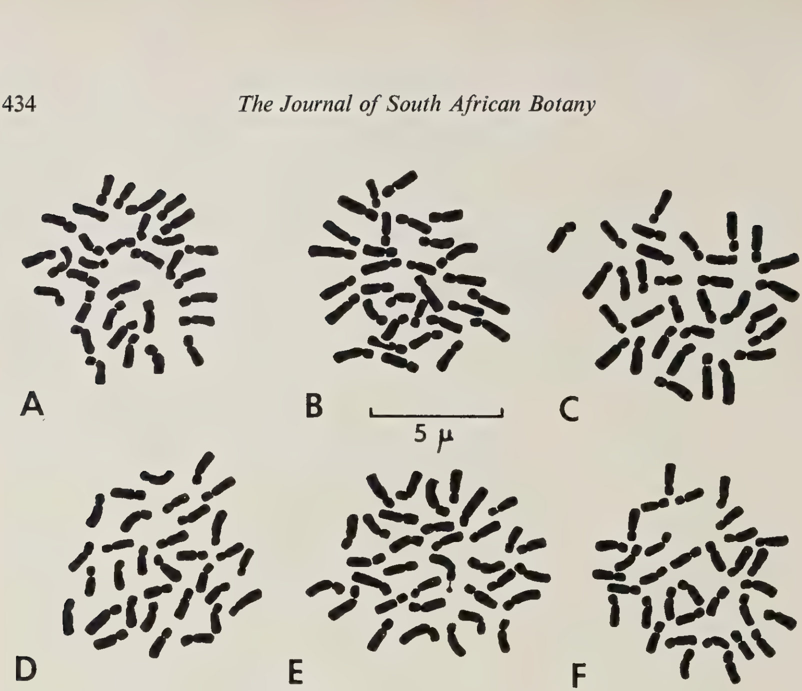

Fig. 31.

Karyotypes of *Tritoniopsis* and *Anapalina*. A. *Tritoniopsis* leslei; B. *T. lata;* C. *T. parviflora;* D. *T. unguicularis;* E. *Anapalina nervosa;* F. *A. triticea.*

a spongy testa and a wing. All the species in the two genera are summer flowering whether they occur in the summer or winter rainfall areas. This is unusual in the *Iridaceae*, especially as the great majority of species occur in the winter rainfall region.

Lewis (1954) suggested that *Tritoniopsis* and *Anapalina* were members of a single phylogenetic line in which *Tritoniopsis* was the more primitive. This seems reasonable, for as she points out, *Tritoniopsis* appears to be less specialised both in the flower and the inflorescence. Branching of the peduncle is common in *Tritoniopsis* but does not occur in *Anapalina*. The flower is either regular or slightly zygomorphic with a short perianth tube in *Tritoniopsis*. In contrast the flower in *Anapalina* is extremely zygomorphic with perianth parts of different lengths, a long curved perianth tube which has an unusual narrow basal portion and an expanded upper portion. This feature of the perianth tube is paralleled in *Homoglossum*, *Petamenes*, *Anaclanthe* and *Antholyza*, and this prompted Hutchinson (1934) to place these genera in a separate tribe apart from the less specialised genera which they otherwise resemble.

Tritoniopsis and *Anapalina* have a series of characteristics which make them appear a quite distinct group of the *Ixieae*. There do not seem to be any morphological similarities with other genera that point to a phylogenetic relationship, nor do cytological features help in this respect. The cytological data confirm that these two genera belong within the tribe *Ixieae* on general size of chromosomes. The diploid numbers of 32 and 34 encountered in these genera are the highest found in the tribe and the karyotypes are perhaps most similar to *Gladiolus* and its allies ($2n = 30$). However, morphological evidence will not support any suggestion of a relationship here.

Anapalina and *Tritoniopsis* are clearly a pair of closely related genera sharing many unique morphological features and having distinct yet similar karyotypes. As suggested by Lewis (1954) these genera form a distinct subtribe which she called *Exohebineae*, a name based on *Exohebea*, a genus now incorporated in *Tritoniopsis*. It seems plausible in the light of Lewis' suggestions on the evolution of the group, that *Anapalina* evolved from an ancestor rather like *Tritoniopsis* in a process which involved the increase in chromosome number, i.e. increasing aneuploidy. In the light of this suggestion it would be interesting to try to breed intergeneric hybrids and observe their meiotic behaviour. This will prove a difficult undertaking as both *Tritoniopsis* and *Anapalina* are notoriously difficult to cultivate and their natural habitat is often rather isolated as they usually grow at high altitudes.

5. SUMMARY OF TAXONOMIC PROPOSALS

a. CLASSIFICATION OF THE FAMILY INTO TRIBES AND SUBTRIBES

It is suggested that the division of the family into three tribes be followed. The tribes proposed by Bentham & Hooker are supported except for the exclusion of one subtribe (*Croceae*) from their second tribe. Their definition of the tribes on the nature of the inflorescence and secondarily, on the position of the stamens relative to the style branches can be correlated with marked differences in chromosome size in these groups. The proposed system is illustrated diagrammatically in figures 32 and 33.

Tribe 1. **Sisyrinchieae** Bentham & Hooker.

Stamens alternate to stigma lobes; style unbranched or branched; branches entire; inflorescence consisting of cymes enclosed in large bracts, and variously grouped together; rootstock unmodified or a rhizome. Chromosomes small or medium in size.

The southern African genera can be treated as comprising two subtribes distinguished on both morphological and cytological grounds. Neither Weimarck nor Lewis can be followed in their placing of the woody genera in a separate tribe, as the cytology reveals that they are allied to *Aristea*.

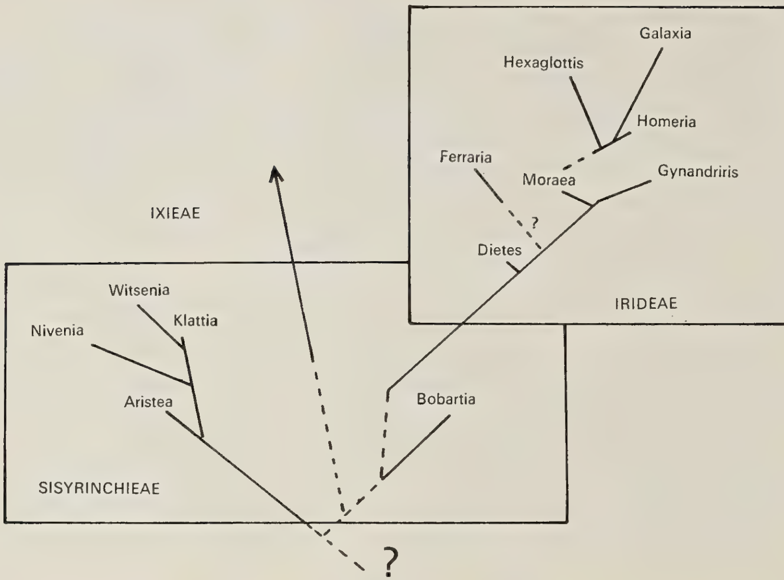

FIG. 32.

Diagram showing suggested phylogenetic inter-relationships of the tribes of the Iridaceae. The relationship of the South African representatives of the Irideae and Sisyrinchieae is also shown.

Subtribe 1. **Aristeineae** Bentham & Hooker (as *Aristeae*)

Style undivided or shortly branched; flowers fugaceous or long lived; rootstock a creeping rhizome or an erect woody stem. Chromosomes small, basic number 16.

Genera recognised: Aristea, Nivenia, Witsenia, Klattia. The latter three genera are woody and exhibit secondary growth. This subtribe may also include several Australian genera such as *Patersonia* (n = 12).

Subtribe 2. **Sisyrinchiineae**

Style branched; flowers fugaceous; rootstock a creeping rhizome. Chromosomes small to medium sized, basic chromosome number 10 in *Bobartia.*

Genera recognised: Only one South African representative, *Bobartia.* This genus is included in this tribe of predominantly New World elements but it may later be found that it should be referred to a separate monotypic subtribe of its own.

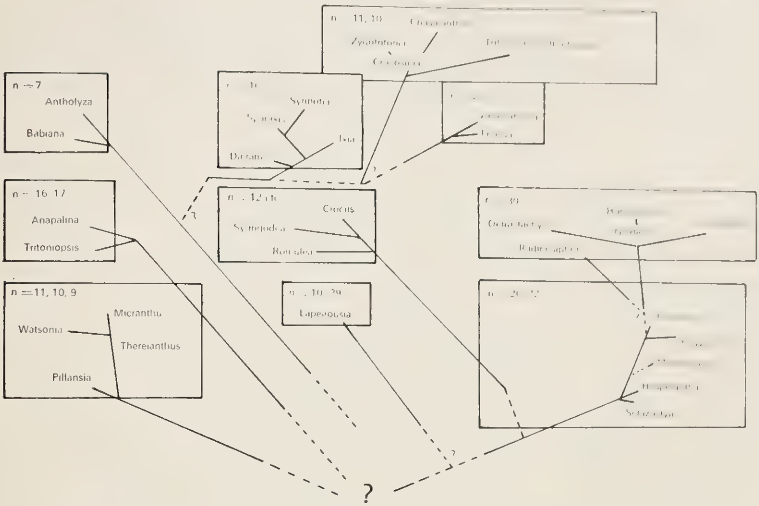

FIG. 33.

Diagrammatic representation of the phylogeny and inter-relationships of the genera of the tribe Ixieae. Each subtribe is contained within a block.

Tribe 2. **Irideae**

Stamens opposite style branches; style usually branched and branches divided; inflorescence consisting of cymes enclosed in large bracts, and grouped together variously, flowers occasionally solitary; rootstock a rhizome, bulb or single internode corm. Chromosomes characteristically large.

This tribe (the *Moraeeae* of Bentham & Hooker) comprises both African, European and New World elements. The African genera are suggested as comprising three subtribes.

Subtribe 1. **Iridineae**

Style three-branched, petaloid, branches terminating in two crests; perianth segments unguiculate, and inner usually erect and smaller than outer; limb of outer segments reflexed; rootstock a rhizome, bulb or corm; stamens free or filaments connate. Chromosomes large, basic number 10 but many other numbers occur.

Genera recognised: Dietes, *Moraea*, *Gynandriris* in Africa and *Iris* and its close allies in the northern hemisphere. Suggestions that *Dietes* be placed in *Moraea* and that *Gynandriris* be transferred to Iris are shown on cytological and morphological grounds to be incorrect.

Subtribe 2. **Homeriineae** Goldblatt subtribes nov.

Stylus subpetaloideus, ramosus et befidus vel non petaloideus et simplex aut profunde divisus; perianthii segmenta subaequales, segmenta non unguiculata interiora non erecta; caudex cormus; filamenta connata. Chromosomata magna, numeri basici 6 et 8.

Type genus: *Homeria* Vent.

Style subpetaloid branched and forked or not petaloid and simple or deeply divided; perianth segments not unguiculates, subequal, inner segments not erect; rootstock a tunicate corm; filaments connate. Chromosomes large, basic numbers 6 and 8.

Genera recognised: Homeria, Hexaglottis, Galaxia.

Subtribe 3. **Ferrariineae** Goldblatt subtribus nov.

Stylus petaloideus, tribus ramis, apice plumoso; perianthii segmenta subaequales, segmenta reflexa; caudex cormus persistens, munitus tunicis tenuioribus; filamenta connata. Chromosomata magna, numerus basicus 10.

Type genus: *Ferraria* L.

Style petaloid, three branched with a dissected feathery apex; perianth segments subequal, reflexed; rootstock a corm; filaments connate. Chromosomes large, basic number 10.

Genera recognised: Ferraria.

This may be allied to several New World genera such as *Tigridia* but further investigation is needed. Differences in cytology and morphology are such that they do not in the author's opinion, support any contention that *Tigridia* is closely related to *Ferraria.*

Tribe 3. **Ixieae** Bentham & Hooker

Style always branched; inflorescence usually a spike (of solitary cymes), sometimes reduced to a single flower; rootstock usually a several internode corm (a rhizome in one genus). Chromosomes characteristically small.

Mainly an African group with only three genera known to extend into Europe and Asia. The subtribes are recognised on cytological grounds but also on correlated morphological features which often are very characteristic.

The subtribes are sometimes difficult to define morphologically when there are only rather minor features to distinguish them.

Subtribe 1. **Watsoniineae** Lewis ex Goldblatt subtribus nov.

Rami styli fucati; cormus rotundus vel aplanatus munitus tunicis reticulatis fibris tenacis; folia equitantia, usitate tenaces et fibrosa. Numeri basici chromosomatum 11, 10, 9.

Type genus: *Watsonia* Miller.

Characterised by bifid style branches; corms rotund to flattened with reticulate tunics of coarse, tough fibres; leaves equitant, usually tough and fibrous; flowers usually arranged distichously. Basic chromosome numbers 11, 10, 9.

A decreasing aneuploid series is suggested in the group where each genus with a lower basic number has a more modified structure.

Genera recognised: Pillansia, Thereianthus, Micranthus, Watsonia. The proposed subtribe *Pillansiineae* of Lewis is not recognised, but is included here.

Subtribe 2. **Lapeirousiineae** Goldblatt subtribus nov.

Rami styli furcati; cormus campanulatus base plana, munitus tunicis duris lignosis, paginis asperis atque base plana integra; folius basalis solum unus, lanceolatus costatus. Numeris basici chromosomatum 10, 9?

Type genus: *Lapeirousia* Pour.

Style branches bifid; corms campanulate, flat based with tunics of hard woody material with a rough surface, also flat based and entire; basal leaf one only, lanceolate and ribbed. Basic chromosome numbers 10, 9?

Genera recognised: Lapeirousia sensu stricto (not including *Anomatheca*).

The subgenus *Anomatheca* included by Baker in *Lapeirousia* has been reinstated as a genus. Its affinities are with *Freesia* rather than with *Lapeirousia*, as evidenced by morphological and cytological data. *L. fistulosa* previously referred to the subgenus *Ovieda* of *Lapeirousia* was shown to be a member of *Anomatheca*, and has been transferred to this genus.

Subtribe 3. **Hesperanthineae** Goldblatt subtribus nov.

Rami styli integri vel longiores stylis vel breviores; caudex rhizome brevis vel cormus campanulatus base plana, asymmeticus radicibus emergentibus crestis lateralis exceptus *Melasphaerula*, tunicis duris integris lignosis paginis laevis; folia equitantis ad teretia vel cruciformia, pauces ad plures. Numerus basicus chromosomatum 13 sed 11 in *Melasphaerula*.

Type genus: *Hesperantha* Ker.

Style branches entire and either longer or shorter than the style; rootstock a short rhizome or a campanulate, flat based and asymmetric corm with the roots emerging from a lateral crest except in *Melasphaerula*, tunics hard, woody and entire with a smooth surface; leaves equitant to terete or cruciform, few to many. Basic chromosome number 13, to 11 in *Melasphaerula*.

Genera recognised: Schizostylis, Hesperantha, Geissorhiza, Engysiphon and *Melasphaerula*.

Subtribe 4. **Crocineae** Bentham & Hooker (as *Croceae*)

Style branches various, unbranched, bifid or multifid; corms asymmetric to symmetric, variously shaped, tunics entire, woody, sometimes papery or fibrous in *Crocus;* leaves slender and modified, either four channelled or terete or bifacial. Inflorescence reduced and flowers solitary on branches or inflorescence unbranched and aerial peduncle lacking; somatic chromosome number varied, and aneuploidy very common. Chromosomes small but often very large in Crocus. Suggested original basic number 12.

Genera recognised: Romulea, Syringodea, Crocus. The latter genus has been included here although this genus is the exception in the tribe, some species having very large chromosomes.

Subtribe 5. **Gladiolineae** Goldblatt subtribus nov.

Rami styli integri usitate expansi in lamella bilobata; cormus rotundus munitus tunicis vel duris marginibus basalis serratis vel papyraceis integrisque; folia vel plures et ensiformia vel unus, gracilis et linearis; bractea usitate magna, herbacea; semina usitate alata. Numerus basicus chromosomatum 15.

Type genus: *Gladiolus* L.

Style branches entire, usually expanded into a bilobed lamella; corm spherical, tunics either hard and split at the basal margins or papery and entire; basal leaves either many and ensiform or single, slender and linear; bracts herbaceous; flowers usually secund, seeds usually winged. Basic chromosome number 15.

Genera recognised: Gladiolus, Homoglossum, Oenostachys, Anomalesia and *Radinosiphon.*

There have been several treatments of the group of genera allied to *Gladiolus.* The genera recognised here are all closely related to *Gladiolus*, and given generic rank for the sake of convenience. Some reduction in the number of genera has been made and the following are changed in circumscription.

(i) *Homoglossum* is maintained, including *Petamenes abbreviatus*, the type species for the latter genus.

Homoglossum can be distinguished as follows: perianth tube long, basal portion slender widening abruptly to a tubular upper portion with a sac at the junction; leaves only one, slender, usually cruciform in section: corms small and having rather woody serrated outer tunics.

(ii) *Oenostachys* is enlarged to include the remaining species of *Petamenes* except *P. buckerveldii* which it is proposed be transferred to *Gladiolus.*

(iii) *Anomalesia* is also enlarged to include the monotypic genus *Kentrosiphon.*

(iv) *Gladiolus* itself is expanded to include the tropical African genus *Acidanthera.*

Subtribe 6. **Ixiineae**

Style branches entire with variously expanded apices; corm spherical with tunics of reticulate fibres of various thickness; leaves several, ensiform; bracts membranous, often dry and lacerated; seeds round and often shiny. Basic chromosome number 10.

Genera recognised: Dierama, Ixia, Sparaxis and *Synnotia.*

The last genus is maintained tentatively on rather doubtful grounds of convenience.

Subtribe 7. **Freesiineae** Goldblatt subtribus nov.

Rami styli furcati; cormus rotundus vel conicus munitus tunicis reticulatis fibris tenuibus; folia duo ad plures, equitantes, ensiformia, molles; capsula usitate pagina aspera; semina rotunda, nitida. Numerus basicus chromosomatum 11.

Type genus: *Freesia* Klatt

Style branches forked; corm spherical to conic with tunics of fine reticulate fibres; leaves two to many, equitant, ensiform, soft in texture; capsule usually with a rough surface bearing round shiny seeds. Basic chromosome number 11.

Genera recognised: Freesia, Anomatheca (previously regarded as a subgenus of *Lapeirousia*).

Subtribe 8. **Tritoniineae** Goldblatt, subtribus nov.

Rami styli integri vel apices bifidi; cormus rotundus ad aplanatus munitus tunicis fibris reticulatis; folia plures, equitantia, usitate molles. Numerus basicus chromosomatum 11 sed 10 in *Chasmanthe.*

Type genus: *Tritonia* Ker.

Style branches entire or slightly divided at the apex; corm round to flattened with tunics of reticulate fibres; leaves several, equitant and usually soft in texture. Basic number 11 but 10 in *Chasmanthe.*

The genus *Curtonus* has been incorporated in *Crocosmia* on grounds of morphological as well as cytological similarity. Two genera, *Montbretiopsis* and *Zygotritonia* which were not examined cytologically by the present author are believed to be allied to *Tritonia* and are included in this subtribe. Further examination may reveal that the monotypic *Montbretiopsis* should be included in *Tritonia.*

Genera recognised: Tritonia, Crocosmia (including *Curtonus*), *Chasmanthe, Zygotritonia* and *Montbretiopsis.*

Subtribe 9. **Babianineae** Lewis ex Goldblatt, subtribus nov.

Rami styli integri; cormus rotundus munitus tunicis subintegris, tenacis; folia ensiformia, plicata, usitate pubescentes. Numerus basicus chromosomatum 7.

Type genus: *Babiana* Ker.

Style branches entire; corm spherical with papery, tough almost entire tunics; leaves ensiform but almost always pleated and pubescent. Basic chromosome number 7.

Genera recognised: Babiana, Antholyza (including *Anaclanthe*).

The genus *Anaclanthe* is incorporated in *Antholyza*, for although it resembles *Babiana* as well, its extreme zygomorphy indicates that it is best included in *Antholyza*.

Subtribe 10. **Exohebineae** Lewis ex Goldblatt, subtribus nov.

Rami styli usitate integri, graceles; cormus magnus, rotundus munitus tunicis reticulatis fibris; folia prominentibus nervis, usitate lanceolata basi gracile, petioloidea; bractea externa proprie brevior quam interna; semina saepe inflata. Numeri basici chromosomatum 16, 17.

Type genus: *Tritoniopsis* L. Bolus.

Style branches usually entire and slender; corms large, spherical with very matted tunics of coarse fibres; leaves usually lanceolate with a slender petiole-like base, bearing several prominent veins; outer bracts characteristically shorter than the inner; seeds often with an inflated testa. Basic numbers 16, 17.

Genera recognised: Tritoniopsis (including *Exohebea*) *Anapalina*.

b. NEW NAMES PROPOSED AS A RESULT OF THE PRESENT STUDY

1. The subgenus *Anomatheca* is recognised here as a valid genus. The following taxonomic changes are necessary:

Anomatheca verrucosa (Vog. in Trew) Goldblatt comb. nov.
Ixia verrucosa Vog. in Trew, Pl. Rar. t 24 (1784), basionym.
Anomatheca juncea (L.f.) Ker in K. & S. Ann. Bot. 1: 227 (1805).
Lapeirousia juncea (L.f.) Ker in Bot. Mag. t 606 (1803).
Gladiolus junceus L.f. Suppl.: 99 (1781) non Burm.f. (1768).

The basionym of *Anomatheca juncea*, namely *Gladiolus junceus* L.f. is a later homonym of *G. junceus* Burm.f. Accordingly the epithet is illegitimate. The next available synonym is *Ixia verrucosa* Vogel in Trew, which is now taken as the basionym for the new combination.

Anomatheca laxa (Thunb.) Goldblatt comb. nov.
Gladiolus laxus Thunb. Flora Cap.: 15 (1823), basionym
Lapeirousia laxa (Thunb.) N.E.Br. in J. Linn. Soc. Bot. 48: 20 (1928)

Anomatheca fistulosa (Spreng. ex Klatt) Goldblatt comb. nov.

Ovieda fistulosa Spreng, ex Klatt in Linnaea 32: 781 (1863) basionym.
Lapeirousia fistulosa (Spreng, ex Klatt) Bak. in J. Linn. Soc. Bot. 16: 155 (1877)

Anomatheca grandiflora Bak. in Journ. Bot. 5: 337 (1876)
Lapeirousia grandiflora (Bak.) Bak. in Bot. Mag.: t. 6924 (1887)

Anomatheca viridis (Ait.) Goldblatt comb. nov.
Gladiolus viridis Ait., Hort. Kew. ed. 1, 3: 481 (1789), basionym.
Lapeirousia viridis (Ait) L. Bol. in S. Afr. Gard. 22: 276 (1932).

2. The circumscription of several genera in the *Gladiolineae* has been altered. The following name changes are made :

Gladiolus buckerveldii (L. Bol.) Goldblatt comb. nov.
Antholyza buckerveldii L. Bol. in Ann. Bol. Herb. 4: 118 (1927) basionym.
Petamenes buckerveldii (L. Bol.) N.E. Br. in Tr. Roy. Soc. S. Afr. 20: 276 (1932)

Homoglossum abbreviatum (Andr.) Goldblatt comb. nov.
Gladiolus abbreviatus Andr., Bot. Rep.: t. 166 (1801) basionym.
Petamenes abbreviatus (Andr.) N.E. Br. in Tr. Roy. Soc. S. Afr. 20: 276 (1932)

Anomalesia saccata (Klatt) Goldblatt comb. nov.
Kentrosiphon saccatus (Klatt) N.E. Br. in Tr. Roy. Soc. S. Afr. 20: 276 (1932)
Anisanthus saccatus Klatt in Linnaea 35: 300 (1868) basionym.

In spite of the large number of described species of *Kentrosiphon*, the author recognises only one, but supports the variety proposed by Obermeyer (1961).

Oenostachys zambeziacus (Bak.) Goldblatt comb. nov.
Antholyza zambeziacus Bak. Handbk. Irid.: 232 (1802)
Petamenes zambeziacus (Bak.) N.E. Br. in Tr. Roy. Soc. S. Afr. 20: 277 (1932)

Oenostachys huillensis (Welw. ex Bak.) Goldblatt comb. nov.
Antholyza huillensis Welw. ex Bak. in Tr. Lin. Soc. Bot. ser. 2, 1: 270 (1880), basionym.
Petamenes huillensis (Welw. ex Bak.) N.E. Br. in Tr. Roy. Soc. S. Afr. 20: 276 (1932).

Oenostachys vaginifer (Milne-Redhead) Goldblatt comb. nov.
Petamenes vaginifer Milne-Redhead in Hook. Ic.: t. 3478 (1951), basionym.

Several other species at present referred to *Petamenes* should also be transferred to *Oenostachys*, but without a knowledge of these and in the absence of material the author prefers not to do so for fear of adding unnecessary synonyms to the literature. For the same reason no species of *Acidanthera* has been transferred to *Gladiolus*.

3. *Curtonus* has been shown to be closely allied to *Crocosmia* and is incorporated in that genus:
   Crocosmia paniculata (Klatt) Goldblatt comb. nov.
   Antholyza paniculata Klatt in Linnaea 35: 379 (1868) basionym.
   Curtonus paniculatus (Klatt) N.E. Br. in Tr. Roy, Soc. S. Afr. 20: 270 (1932)

4. The genus *Anaclanthe* is incorporated in *Antholyza.* The following treatment is necessary:
   Antholyza plicata L.f. Suppl.: 96 (1781)
   Anaclanthe plicata (L.f.) N.E. Br. in Tr. Roy, Soc. S. Afr. 20: 269 (1932).

   Antholyza namaquensis (N.E. Br.) Goldblatt comb. nov.
   Anaclanthe namaquensis N.E. Br. in Tr. Roy. Soc. S. Afr. 20: 269 (1932) basionym.

6. THE SIGNIFICANCE OF CYTOLOGICAL DATA IN THE IRIDACEAE

General discussion on the cytology of the Iridaceae and the significance of some cytological features.

6.1 POLYPLOIDY

It has been estimated by Stebbins (1950) that the proportion of polyploid species in the Angiosperms may be about 35%, but this figure is perhaps rather conservative judging by the data quoted by Reese (1957). In view of this, the number of polyploid species in the southern African Iridaceae is surprisingly low, for of the approximately 300 species which have been cytologically examined, only some 20 are polyploid. Of these, only 13 occur in the south-western Cape Province where the concentration of species is greatest, and where almost 250 of the studied species occur (Table 18, 19).

The distribution of polyploidy in different families and geographical areas varies considerably. In general, it has been observed to increase with latitude in the northern hemisphere (Reese 1957) though Stebbins has pointed out that changes in the composition of the flora usually accompany increase in latitude and that families where polyploidy is more frequent often become more common. The correlation between increased latitude and polyploidy does, however, still appear correct but to a smaller extent than previously suggested, when floral composition is taken into account.

A similar correlation between latitude and polyploidy was observed by Manton (1952) in the fern flora of Madeira and Britain, where polyploidy increases from 42% to 53%. Subsequently, she found the frequency of polyploidy to be 60% in the ferns of Ceylon (Manton 1953). This appears to indicate that it may not be latitude and the accompanying cold conditions that are the critical factor. Manton proposed that the observation could be explained on the basis

of the disturbance of flora. Ceylon, which has a stratified flora, has a high rainfall and is subject to flood and landslide which disturb normal habitats and enable species not usually sympatric to grow near one another and hybridise. The suggested disturbance factor in the northern hemisphere is the extreme prehistoric glaciation which probably had a more marked effect on the environment than landslide and flood.

An increase in altitude would be expected to have a similar effect and this has been observed by Morton (1964), who showed that a representative sample of the flora of West Africa had 26% polyploidy while the tropical African mountains, Kilimanjaro and Mt. Cameroon had 47% polyploidy (compared to 38% in the northern Sahara and 70% in Greenland). The mountain regions have been partly glaciated at times and Morton suggested that environmental instability was the factor favouring increased polyploidy. Even when it is realised that the floral composition varies in the above areas, the correlation seems relevant.

The occurrence of polyploidy is known to vary greatly in different families. According to Stebbins (1956) it is particularly high in the Gramineae (70%) and also in the Cyperaceae, Rosaceae and Iridaceae amongst others, but absent from families such as the Curcurbitaceae, Fagaceae, Moraceae. It occurs commonly in some genera in a family and not others e.g. in the Salicaceae it occurs in *Salix* but not in *Populus*. In general it is most common in perennial herbs, less frequent in annuals and rare in woody plants. Stebbins' view that polyploidy is common in the Iridaceae can, in the light of the present study, be seen as incorrect but his information must have been based on northern hemisphere genera like *Iris* and *Crocus* where it is common.

An analysis of polyploidy in the Iridaceae shows similar inconsistencies in its distribution. Polyploidy is almost absent from the southern African members of the tribe *Sisyrinchieae*. *Aristea ecklonii* is one species which must be accepted as consistently polyploid, but in *A. glauca*, where a polyploid population was discovered, the polyploidy does not seem to be significant and is possibly a case of isolated autoploidy. *A. ecklonii* is a summer rainfall species, occurring along the eastern mountains of southern Africa.

Sisyrinchium, a New World genus, which occurs from Uruguay to Greenland, exhibits a high degree of polyploidy. This increases in both frequency and level in different species with an increase in altitude and latitude (Böcher, 1966). In contrast, no polyploid species have been found in *Bobartia*, believed to be a close ally of *Sisyrinchium*, and which occurs only in South Africa.

Polyploidy is also relatively uncommon in the southern African representatives of the Irideae and is absent from some genera. The highest frequency was observed in *Ferraria* and *Gynandriris* where one of the three species studied in each genus was polyploid. The polyploid species of *Gynandriris* is, however,

unusual in its distribution, being the only member of the genus recorded for the northern hemisphere. In some of the other genera approximately a quarter of the species studied are polyploid, though in *Moraea* less than a tenth of those examined proved to be polyploid, and no polyploid species have been found in *Hexaglottis*.

Iris, which is widespread in the northern hemisphere and closely related to *Moraea*, is by contrast cytologically complex. It is clear that many species of *Iris* have a polyploid origin while others have evolved by aneuploidy from them. If these are also considered as polyploid, then the frequency is above 50% in this genus as a whole, though according to Simonet (1934) polyploidy is apparently absent in some sections of the genus.

It seems clear that in these two tribes, the *Sisyrinchieae* and *Irideae*, the potential for polyploidy is present but occurs only under certain conditions, the most obvious of which are increases in frequency with latitude in the northern hemisphere and to a lesser extent with altitude. This correlation is clearly in accord with previously accepted views and in *Iris* particularly, glaciation has been proposed to explain the phenomenon.

In the third tribe, the *Ixieae*, polyploidy is very uncommon. This tribe is predominantly African in occurrence though three genera are found in Europe and Asia. The majority of genera, however, occur exclusively in the south-western Cape Province and it is here, where polyploidy is most rare, that the majority of species occur. The observation in the other tribes, that the number of polyploid species is greater in the northern hemisphere is also noted for the *Ixieae*. All the species of *Gladiolus* occurring in Europe and Asia are high polyploids, while lower polyploids occur in the central African mountains and no polyploids at all are recorded from the south-western Cape Province. *Crocus* a fairly large genus, exhibits the greatest degree of polyploidy in the *Ixieae*, and it is almost exclusively European and Asian in distribution. As in *Iris*, several species have a polyploid origin, while others seem to have originated by aneuploid changes. The frequency of polyploid species has been established to be higher than 50% by some workers.

A possible explanation for the scarcity of polyploid species in the *Ixieae* in southern Africa and in the western Cape Province particularly, can be offered. Firstly the species do not appear to have one of the major requirements for polyploid speciation, hybrid infertility. It is well known (see section on inter-generic hybridisation) that interspecific hybrids can be obtained with ease in many of the genera, and that the hybrids are fertile so that genetic segregation occurs in the following generations. Secondly, the majority of species are endemics, particularly in the south western Cape Province where many of the species in the *Ixieae* are very localised.

It is suggested that much of the speciation in this group is fairly recent and that this has occurred almost entirely at the diploid level. If this is correct, then most species are fairly young and may not yet have developed internal barriers to reproduction which would cause hybrid sterility. It must be pointed out, however, that even in *Gladiolus* where polyploid species do occur, a degree of hybrid sterility is not a common phenomenon and most species appear to be interfertile.

In the *Ixieae* a single species each, of *Tritonia* and *Ixia*, were found to be polyploid and in both cases they were summer rainfall species. Two of the three polyploid species of *Romulea* found by de Vos (1965) in South Africa and the

TABLE 18

The frequency of polyploid species in the African genera of the Iridaceae, with comparisons to the non-African genera *Iris*, *Crocus* and *Sisyrinchium*. The approximate total number of species in the genus, the number that have been cytologically studied and the number of polyploid species in toto and in winter rainfall areas are given.

GENUS	Total No. Species	No. cyt. examined	No. polypld. species	No. polypld. species in winter rain-fall area.
(SISYRINCHIEAE)				
Aristea	50	11	1	0
Nivenia	8	3	0	0
Klattia	1	1	0	0
Witsenia	1	1	0	0
Bobartia	12	3	0	0
Sisyrinchium	75	25	20	—
(IRIDEAE)				
Moraea	60	27	2	1
Dietes	6	4	1	0
Homeria	30	12	3	2
Galaxia	5	4	1	1
Gyandriris	10	3	1	0
Hexaglottis	4	2	0	0
Ferraria	10	3	1	1
Iris	200	(Not known exactly; estimated more than 50% polyploid.)		
(IXIEAE)				
Gladiolus	150	46	8	0
Romulea	90	±32	3	1
Geissorhiza	48	11	3	3
Tritonia	40	10	1	0
Ixia	44	14	1	0
Watsonia	70	20	1	1
Pillansia	1	1	1	1
Other African genera	±300	±100	0	0
Crocus	60	(Not known; estimated that 50% of species are polyploid)		

few African species of *Gladiolus* that are polyploid also occur in the summer rainfall area. As can be seen from Table 19, the frequency of polyploid species in the summer rainfall area is about 30%.

Only six species of *Ixieae* in the winter rainfall area were found to be polyploid, three of which belong to the genus *Geissorhiza*, one to *Watsonia* and one to *Pillansia*, suggested to be a relict polyploid. To this number, one species of *Romulea* can be added as judged from the chromosome numbers given by de Vos (1965) for that genus. This represents a frequency of about 3%. The correlation of increasing latitude or cold conditions does not seem to explain these striking differences between the southern African summer and winter rainfall species. The suggestion of Manton that the common factor is violent

Table 19

The frequency of polyploidy of the southern African representatives of the tribes *Ixieae* and *Irideae*. The number of species cytologically investigated, the number of polyploid species and the percentage of polyploid species is given and the tribes are divided into species occurring in either summer (s.rf.) or winter (w.rf.) regions.

TRIBE	No. species studied	No. polyploid	Approximate %
Ixieae w.rf.	200	6	3%
s.rf.	38	12	30%
Irideae w.rf.	38	5	12%
s.rf.	17	4	25%

ecological disturbance is equally unsatisfactory for as a group, the species from both areas have similar ecological requirements. They usually grow in cooler areas, often on mountain slopes or plateaux. Both areas have a high rainfall, not noticeably different, nor is either of the areas known to be more geologically unstable or prone to landslides. Yet it remains clear that the frequency of polyploid species is far higher in all tribes in the summer rainfall area and this requires further investigation. The genus *Geissorhiza* seems to be an exception for three of the eleven species proved to be polyploid. The genus occurs only in the winter rainfall area. The reason for the relatively high incidence of polyploidy here also requires investigation.

It is not known whether the low frequency of polyploid species in the Iridaceae also occurs in other groups in southern Africa. Comparable cytological studies are few and not representative of the whole area. The Proteaceae are one family where the cytology has been fairly well studied and no polyploid species have been recorded in southern Africa. Norlindh (1963) found only two polyploids among the southern African species belonging to the tribe *Calenduleae* (Compositae) that he examined and both were summer rainfall representatives.

Ornithogalum (Liliaceae) is perhaps more comparable to the Iridaceae, being a perennial geophytic genus which, though widespread in South Africa, is more common in the winter rainfall region. Here polyploidy is extremely rare and perhaps only two true polyploid species occur out of thirty that have been investigated (Pienaar 1963). In the case of *Ornithogalum* both polyploid species occur in the winter rainfall region.

More cytological studies on African plants are obviously required before comments can be made about polyploidy in this part of the world. Except for the Iridaceae, comparisons are not yet possible between African and non African plants and until such studies are made, it will not be possible to observe any general trends.

6.2 CHROMOSOME NUMBER

There is considerable variation in chromosome number at the diploid level in the Iridaceae. Most genera are characterised by a particular number but aneuploidy occurs in *Sisyrinchium*, *Iris*, *Moraea*, *Romulea* and *Crocus*.

Chromosome number is a useful taxonomic and phylogenetic tool where variation occurs and is particularly valuable for genera where aneuploidy is found. The significance of chromosome number *per se* is not clear. A difference in number is a reproductive barrier in closely related species or genera, as it usually results in meiotic abnormalities in hybrids leading to sterility.

The actual mechanism for changes in basic number are known and proved only for decreasing aneuploidy and this has been suggested to be far more common than increase in number. As Jones (1970) has pointed out, various authors have explained the decrease in number as of possible advantage in changed relationships of genes resulting in new adaptive complexes and in the general tightening of linkage relationships.

Whether there is in fact any significance in the chromosome number in the family, it would seem that ancestral polyploidy can be discounted, for as discussed under the section on chromosome size, the quantity of chromosome material is very similar in all the genera of the *Ixieae* (disregarding polyploid species). The same can be said for the genera of the Irideae though the quantity here is not quite constant. Chromosome number has also been suggested to be of significance in the production of more or less variable offspring, particularly in annuals (Stebbins 1950, 1957). Aspects such as these require investigation in the Iridaceae although chromosome number may be quite without such direct adaptive significance in the family.

The widely held view that a decrease in chromosome number is more common than an increase seems to be confirmed by the present studies in the Iridaceae, but although this has been more common, the opposite process does occur. In the *Irideae* and *Ixieae*, where generic relationships are often fairly

clear, decreasing aneuploidy has occurred in *Moraea*, *Hexaglottis*, in the *Watsoniineae* and possibly in the origin of *Romulea* and of *Chasmanthe*. In *Romulea* itself, decreasing aneuploidy has been more common but there seems little doubt that some degree of increasing aneuploidy has also taken place. Stepwise increase in number also seems to have occurred in the origin of *Gladiolus*, in the evolution of the *Exohebineae* and possibly in the origin of the genus *Galaxia*.

6.3 CHROMOSOME SIZE

The general size of the chromosomes, considered by Stebbins (1950) as a major characteristic of the karyotype, differs considerably in the Iridaceae. Differences in general chromosome size are known in many groups of Angiosperms, though size is, under normal circumstances, constant in a species. Increase in chromosome size in temperate climates is often observed and in some cases also a degree of morphological specialisation (Stebbins 1950). This trend is, however, not general and several exceptions are known. In some genera such as *Lilium*, an adaptive significance has been suggested for the large chromosomes in a cold climate (Stebbins 1966). Nevertheless, as Davis and Heywood (1963) pointed out, generalisations should be avoided and each case should be treated on its merits.

In the Iridaceae there are two distinct series of chromosome sizes with the difference in total chromosome length considerable. This difference has been used by the present author as one of the criteria for the recognition of tribes in the family. The tribe *Sisyrinchieae*, a group with small to medium chromosomes is believed to be the most primitive group in the family. The chromosome size is similar in the *Ixieae* with the exception of *Crocus*. The *Irideae*, a group with large chromosomes, must be regarded as karyologically specialised if the Iridaceae are a natural group which presupposes common ancestry.

Total chromosome volume is a more comparable measure than length because it takes into account the variation in width of chromosomes. It is believed to be directly proportional to the quantity of DNA present in the nucleus (Sparrow & Miksche 1961). Chromosome volume in selected genera in each of the tribes is compared in Table 20. Here the volume has been calculated by assuming the chromosomes are cylindrical and using the formula $\pi r^2 h$ where r is the radius or half the width, and h the total length of the chromosomes. There is probably some degree of error in measurement, particularly in width which is of the order of between 0,5 and 1,0μ. The error here may be about 10%. The length has been calculated by determining the average of the length of several karyotypes. This measure of chromosome size, though possibly prone to a considerable degree of error, seems to the present author a more meaningful measure than length alone, as used for example by Rothfels *et al.* (1966) in their study of the chromosome cytology of *Anemone*.

These calculations show that in spite of considerable variation in chromosome number in the groups with small chromosomes, both *Aristea* and members of the *Ixieae* have a similar chromosome volume and presumably the same quantity of DNA. In the *Irideae* the chromosome volume is more variable with a range from 40 to 90 cubic μ. Some of the smaller differences here may be ascribed to error, for small differences in the width would affect the result considerably but it is clear that error alone cannot account for the very high figure obtained for several species of *Moraea* with a diploid number of 12, e.g. *M. spathulata.* The remainder of the genera, including species of *Moraea* with diploid numbers of 20, have a similar chromosome volume and probably form a single group.

The high figures obtained for several of the species of *Moraea* suggests polyploidy but this does not seem possible as these have the lowest diploid number encountered in the genus. A possible explanation is that the DNA is arranged in the chromosome in a less dense manner or that the chromosomes

TABLE 20

A comparison of chromosome size in some genera and species of the South African Iridaceae. The basic number, total chromosome length, width, radius squared and total volume of each selected genus or species is shown.

Tribe & genus or species	Somatic Number	Total Chro. Length. μ	Chro. Width. μ	Radius^2 (to three decimal places)	Volume $\pi r^2 h$ μ^3
SISYRINCHIEAE					
Aristea	32	40	0,5	0,063	7,8
Bobartia	20	80	0,6	0,09	22,6
IXIEAE					
Tritonia	22	40	0,5	0,063	7,9
Babiana	14	38	0,5	0,063	7,5
Therianthus . . .	20	40	0,5	0,063	7,9
Watsonia . . .	18	40	0,5	0,063	7,9
Ixia	20	38	0,5	0,063	7,5
Sparaxis	20	36	0,5	0,063	7,0
Hesperantha . .	26	40	0,5	0,063	7,9
Gladiolus . . .	30	36	0,5	0,063	7,0
IRIDEAE					
Dietes	20	100	0,75	0,14	45
Moraea spathulata (2n=12) . . .	12	100	1,1	0,3	95
M. ramosissima (2n=20) . . .	20	110	0,75	0,14	50
M. ciliata (2n=20) . . .	20	70	0,9	0,2	44
Homeria . . .	12	84	0,9	0,2	53
Galaxia	16	80	0,8	0,16	40
Hexaglottis . . .	12	75	0,9	0,2	47

are polynemic (i.e. multistranded). This same explanation can be offered for the great difference in chromosome volume between the *Ixieae* and *Irideae* where the differences are of the order of six times and suggests a fundamental difference between these groups. Several attempts were made to ascertain whether the difference in size could be attributed to multistrandedness of chromosomes. This condition was sometimes observed in species with large chromosomes but the small chromosomes were themselves too small to observe the condition even if it did occur.

The exceptional genus in the *Ixieae* is *Crocus*, which grows actively under very cold winter conditions. The same cannot be said for the majority of the *Irideae*. Certain species of *Iris* grow in a similar environment to *Crocus*, but none of the other genera of the *Irideae* studied here do, and the large chromosome size cannot be ascribed to the supposed adaptation to cold conditions. *Morea* and *Homeria* grow under the same ecological conditions as the *Ixieae* and appear even to fill similar ecological niches. The difference here is perhaps an ancestral condition that has persisted rather than an adaptive one.

The significance of differences in size of chromosomes remains unclear and there are probably several different explanations in various groups of plants. Multistrandedness and perhaps lateral replication of chromatids are also suggested to occur in some plants, but here the significance is not explained. Further investigation seems fundamental to the understanding of chromosome structure and the genetic and taxonomic significance of size differences remain for the most part unknown.

7. GEOGRAPHICAL DISTRIBUTION

The geographical distribution of the family in relation to cytology and possible phylogeny

Sisyrinchieae

Genera in this tribe are spread throughout the world, but the majority are found in the southern hemisphere. There are three centres of distribution, southern Africa, Australia and South America. The genera occurring north of the equator are *Sisyrinchium* and *Belamcanda*, the latter specialised. In *Sisyrinchium* only polyploid species occur in the northern hemisphere while the South American representatives are diploid or low polyploids.

This tribe, the least specialised in the Iridaceae is apparently of southern origin. It shares with a large number of other groups, e.g. Proteaceae, Restionaceae, this peculiar southern distribution which has been regarded as evidence that the southern continents were at some time in the past part of a single land mass known as Gondwanaland. This evidence of present and past floral

similarity on the southern continents is regarded as evidence for the theory of continental drift, which though much ridiculed by geologists in the past, is now gaining acceptance.

Irideae

This tribe is mainly Central and South American and African but is well represented in Europe and Asia by *Iris* and in Australasia by one species of *Dietes*. Except for *Iris*, and *Tigridia*, the majority of species occurring north of the equator belong to southern genera. *Iris*, which is a somewhat specialised genus, is believed to be derived from the southern genus *Dietes*. Thus this tribe, predominantly southern in distribution, probably also has its origin in the areas believed to have been part of Gondwanaland.

Ixieae

Except for the specialised *Crocus*, the tribe is African in distribution and most of the genera have an exclusively southern range. The cytology and classification are fairly well known and it appears that many of the subtribes have a central African origin.

The distribution of the genera and subtribes has been discussed individually in an earlier section. Of the ten subtribes recognised by the present author, eight are sufficiently well understood to be commented on. In the subtribes *Ixiineae*, *Tritoniinieae* and *Hesperanthineae*, the most primitive genera are distributed irregularly in southern and tropical Africa, being confined to mountain ranges, e.g. *Hesperantha*, *Dierama*. The *Gladiolineae* and *Crocineae* are both believed to be specialised from the *Hesperanthineae* and their most primitive genera occur in the Cape Province. These are believed to have originated in the south western Cape Province and have spread into Africa and Europe where *Romulea* and *Gladiolus* are found. *Crocus*, the predominantly Mediterranean genus believed to be derived from *Romulea* appears to have originated in the eastern Mediterranean region. As already discussed, a reverse origin seems unlikely for the most primitive species in these genera are found in the Cape Province and the European species of *Gladiolus* and *Romulea* are high polyploids.

The *Babianineae* and *Watsonineae* also appear to be southern in origin, for the least specialised species occur in the south western Cape Province. Individual species of *Babiana* occur in Rhodesia and Socotra but in both cases the species are specialised. *Watsonia* also occurs outside the Cape Province, in the eastern mountains as far as the northern Transvaal and in Madagascar, but again these species are more specialised than some found in the Cape Province. The *Exohebineae* are a poorly understood group but also seem to have their origin in the south western Cape Province for it is here that the least specialised species, *Tritoniopsis leslei* occurs.

It appears that the *Ixieae* arose in Africa. Whether Cape or tropical African in origin is not clear for subtribes have clearly originated in both areas. It is suggested that the tribe is primarily Central African in origin though poorly represented there today. With changes in climate and topography over millions of years, the tribe has become confined to tropical African mountain zones or has found refuge in the winter rainfall region of the Cape Province. Here great speciation has occurred which is believed of fairly recent origin. The most specialised tribes appear to have evolved here and some genera have spread from the Cape through Africa to Europe.

8. SUMMARY

The karyotypes of the southern African members of the *Iridaceae* are described and discussed with regard to taxonomy, phylogeny and evolution of the family. The karyotypes of 225 species in 43 genera were investigated, 186 of these being new cytological records.

Hybridisation is discussed in the family with special reference to intergeneric hybrids. Nineteen intergeneric crosses were attempted and five were successful. The significance of the intergeneric crosses is then discussed in relation to the taxonomy of particular genera.

The different systems of classification of the Iridaceae are evaluated, those of Bentham & Hooker, Pax, Hutchinson and Lewis being regarded as the most significant. The cytological evidence is then discussed in relation to the major subdivisions of the family. It was observed that the chromosomes fell into two distinct size groups, small and very large, which were found to correspond to the tribes proposed by Bentham & Hooker, the genera with large chromosomes belonging to the *Irideae* and those with small chromosomes to the *Sisyrinchieae* and *Ixieae* respectively. The genus *Galaxia* with large chromosomes is shown to be incorrectly placed in the *Sisyrinchieae* and Lewis' contention that this genus be placed in the *Irideae* is supported.

The cytological data are discussed at generic level, each tribe being dealt with separately. In general, it was observed that a genus or group of genera have a distinctive karyotype and that this could be linked with certain morphological features. In this way it became possible to determine intergeneric relationships and to recognise subtribes in many cases.

In the *Sisyrinchieae*, *Aristea* with a basic number of 16 is shown to be allied to the woody genera, *Nivenia*, *Klattia* and *Witsenia* also with a basic number of 16. Evidence strongly suggests that these form a single subtribe and should not be placed in different tribes as suggested by Weimarck and by Lewis. *Bobartia* was found to have a basic number of 10 and to have somewhat larger chromosomes than *Aristea*. It is shown to be a natural group itself, but is believed to be only distantly related to *Aristea* and its allies and a separate subtribe is proposed for this group.

In the second tribe, the *Irideae*, *Dietes* is shown to have a basic number of 10 and one species, *D. bicolor* is suggested to be a tetraploid. *Dietes* is suggested as the ancestor of both *Iris* and the genus *Moraea* and is shown to be intermediate between these two genera so that it cannot correctly be included in either. An ancestral basic number of 10 is suggested for *Iris* and for *Moraea*.

A large number of species of *Moraea* were studied and this genus was found to be heteroploid with haploid numbers of 10, 9 and 6. *M. ramosissima* with a basic number of 10 is suggested as the ancestral type of the genus and is linked to *Dietes*, which has a similar karyotype. The classification of *Moraea* into sections and subgenera by Baker is reviewed and is in general confirmed, though a few species were found to be misplaced.

Two representatives of the genus *Gynandriris* were studied and found to have a karyotype like that of the previously studied European species which is shown to be polyploid. The karyotype of the genus is found to be very similar to that of some species of *Moraea*. The treatment of Lawrence in placing the European species of *Gynandriris* in *Iris* is shown to be inconsistent with the maintenance of *Gynandriris* and *Moraea* in South Africa, genera to which the European species of *Gynandriris* is clearly more closely allied.

Several representatives of the genus *Homeria* were studied and the basic number was found to be 6. One species *H. breyniana* was found to be tetraploid and a variety of this species (var. *aurantiaca*) to be hexaploid. The similarities between *Homeria* and *Moraea* are discussed and shown to be rather poorly defined but it was concluded that *Homeria* must be maintained if only for convenience.

The genus *Galaxia*, with a basic number of 8, and large chromosomes is shown conclusively to belong to the *Irideae*. Its suggested allies are *Homeria* or *Moraea*. One species, referred to *G. ovata*, was found to be polyploid. *Hexaglottis* was also found to have large chromosomes. One species had a basic number of 6 and the other 5. The latter species, *H. virgata* is suggested to be specialised and to have been derived by aneuploid reduction.

The genus *Ferraria* was found to have a basic number of 10. One species, *F. undulata*, is shown to be consistently hexaploid while the other two that were studied were diploid. It is suggested that *Ferraria* is a specialised offshoot of *Dietes* and not to be allied to the American genus *Tigridia*, which has a different karyotype and morphology.

It is proposed to recognise three subtribes in the South African *Irideae*, one the *Iridineae* being widespread and including *Iris*, *Moraea*, *Dietes* and *Gynandriris*. The *Homeriineae* comprising *Homeria*, *Galaxia* and *Hexaglottis* and the *Ferrariineae* comprising only *Ferraria*, are exclusively southern African in distribution.

The genera in the tribe *Ixieae*, which is characterised by rather small chromosomes can be conveniently divided into ten groups which are designated as subtribes. The cytological data show that Hutchinson's classification of the genera in this group into three tribes based on floral morphology, is incorrect as genera with similar karyotypes and vegetative features are often placed in different tribes in his system. Lewis' classification of this group is found to compare very well with the cytological data though it was found convenient to subdivide one of her proposed subtribes, the *Ixiineae*, into four distinct subtribes. Another of her subtribes, the *Watsoniineae*, is divided into three subtribes which are suggested to be rather distantly related to one another.

In general it is found that the cytological evidence can best be correlated with vegetative features and that the nature of the corm, leaves, bracts and to a lesser extent the nature of the stigma branches, are the most significant features in this respect.

In the first of the subtribes, the *Watsoniineae*, only four genera are recognised including *Pillansia* which Lewis regarded as belonging to a separate subtribe This genus is found to be consistently polyploid and is suggested to be a relict tetraploid. A decreasing aneuploid series is suggested in this tribe leading from *Pillansia* (basic number 11) to *Watsonia* (basic number 9). *Watsonia bulbillifera* is found to be a sterile triploid, reproducing by cormlets alone. A possible ancestry is suggested for this species.

The second subtribe, the *Lapeirousiineae*, comprises only a single genus, *Lapeirousia*. Only two of the recognised subgenera, *Ovieda* and *Sophronia* are admitted to the genus and the third, *Anomatheca* is recognised as a valid genus, allied to the genus *Freesia*. Cytological and morphological evidence is cited to substantiate the differences between *Lapeirousia* proper on the one hand and *Anomatheca* and *Freesia* on the other. One species, previously referred to *Lapeirousia*, *A. fistulosa*, is shown to belong to *Anomatheca*. The tribe *Freesiineae* is proposed for *Anomatheca* and *Freesia*.

The four genera *Geissorhiza*, *Hesperantha*, *Schizostylis* and *Engysiphon* are found to be a natural group, sharing a basic number of 13 and several similar morphological features. *Melasphaerula* with a basic number of 11 is placed with these genera because of several morphological similarities. The subtribe *Hesperanthineae* is proposed for this group. The genus *Geissorhiza* is unusual in that three of the eleven species examined are found to be polyploid.

Lewis' interpretation of the subtribe *Crocineae* Bentham & Hooker (*Romulineae* of Lewis) is supported and it is shown that the three genera in this group are all heteroploid. The position of *Crocus* in this subtribe is questioned as it is the only genus in the *Ixieae* with very large chromosomes, although morphologically it seems to be correctly placed here. The possible origin of *Romulea* is discussed and *Geissorhiza* is suggested as a likely ancestor. Following this suggestion, a basic number of 24 for the genus and subtribe is proposed.

Gladiolus and its suggested allies were studied and all are found to have a basic number of 15. The existence of a polyploid series in the species in the summer rainfall region of Africa and the Mediterranean region is confirmed and on this basis a southern origin of the genus is proposed. All the species in the winter rainfall region of South Africa that have been studied are diploid, and those that are least modified occur here. The suggested origin of *Gladiolus* from *Geissorhiza* is discussed and if correct must have been accompanied by increasing aneuploidy. The occurrence of different levels of polyploidy in some species is mentioned, in particular *Gladiolus natalensis*, where triploid, tetraploid and pentaploid individuals were found in a single population.

The cytological evidence confirms the close relationship of *Acidanthera*, *Radinosiphon*, *Homoglossum*, *Petamenes* and *Anomalesia*, while the morphology of *Oenostachys* and *Kentrosiphon* indicates that these are also allied to this group. Intergeneric hybrids between several of these and *Gladiolus* have been previously recorded or were produced by the author, which confirms the close relationship of these genera. Several changes in circumscription of genera were proposed.

The subtribe *Ixiineae* proposed by Lewis is reduced to comprise only four genera, *Dierama*, *Ixia*, *Sparaxis* and *Synnotia*, all of which share a very similar karyotype. The status of *Synnotia* is critically discussed and it is concluded that it could be included in *Sparaxis* though this step may not be convenient. The possible evolution of this group is outlined.

The new subtribe, *Tritoniineae* is proposed for *Tritonia* and its allies, cytological similarities again pointing to the relationship. The genus *Curtonus* is treated as a species of *Crocosmia*. *Chasmanthe* is placed in this group although it has a slightly different karyotype. Lewis' subtribe *Babianineae* is supported on cytological grounds but *Anaclanthe* is included in *Antholyza* leaving only two genera in this subtribe. The proposed subtribe *Exohebineae* of Lewis is also supported. The two genera in this group have the highest chromosome numbers in the family, barring polyploid species.

The cytology of the family was then discussed in general. Polyploidy, previously believed common in the family, is shown to be rare, especially in the winter rainfall area of the Cape Province. Possible reasons for this are discussed. Chromosome number and size are briefly discussed and the often observed higher frequency of the decreasing aneuploidy is confirmed.

A brief discussion of the geographical distribution of the family led to the suggestion that the family originated in the southern hemisphere, possibly in prehistoric Gondwanaland. The *Ixieae* are suggested to be African in origin with a few representatives in Europe and Asia. The possible origin of some subtribes in the *Ixieae* is outlined.

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Patterns of change in Tropical Plants by G. P. Chapman, with pp. 112, and illustrations. London: University of London Press Ltd., 1970.

This little book makes interesting reading. It is a good introduction to the study of the variation and genetics of plants and is illustrated by examples mostly from tropical and subtropical regions. The examples are mostly cultivated species and the origin of some of them, for example that of the tomato, banana and maize, is discussed at length.

The author in writing this book had undoubtedly in mind a saying of C. G. G. J. van Steenis that "botanical teaching based on the temperate flora must necessarily be ill-balanced and inadequate" (p. 2) and was undoubtedly under the impression of what H. G. Baker describes in the Foreword (p. 9) as "a growing awareness that an understanding of tropical biology is essential before we can comprehend the general principles of evolution and ecology in the world as a whole". In taking plants from the warmer parts of the world into consideration this book is a valuable contribution to a balanced and adequate study of plant variation and plant genetics.

Many of the examples used for illustration are also well known in Southern Africa and in the Southern Hemisphere. This is an additional reason why this little book should appeal to plant biologists in South Africa.

P. G. Jordaan

Physiological Plant Pathology, Vol. 1 no. 1, January, 1971. Edited by T. F. Preece and B. J. Deverall, with pp. i + 83. London and New York: Academic Press. $19.50.

This is the first international phytopathological journal to specialize in a restricted field of this science. Papers will be considered for publication only if they have a bearing on physiological, biochemical, ultrastructural, genetic or molecular aspects of host-parasite interactions, on environmental effects on such relationships and on modifications of host metabolism induced by pathogens. It is thus obvious that the journal is intended mainly for research workers but will also be of great help to teachers in the field.

The first number of Volume I has ensured that this publication will be enthusiastically received by those interested in the host-parasite interrelationship. A pleasing feature is an excellent review by C. H. Beckman on the plasticizing of plant cell walls and tylose formation. The remaining research papers, some by well known authorities, include studies on the hypersensitive reaction induced in tobacco by noncompatible phytopathogenic bacteria, the production and breakdown of phytoalexins, pectic enzymes, virus multiplication, and the effect of light intensity on the infection of wheat by *Septoria tritici*, while J. P. Blakeman and A. K. Fraser reported that antagonistic bacteria inhibit the growth of *Botrytis cinerea* on the surface of chrysanthemum leaves.

In common with other publications of Academic Press, the lay-out of *Physiological Plant Pathology* is of a high standard. A few minor discrepancies were noted in the form in which references were listed, but these can easily be eliminated in future issues.

M. J. Hattingh

Das Sukkulenten Lexikon. Kurze Beschreibung, Herkunftsangaben und Synonyme der sukkulenten Pflanzen mit Ausnahme der Cactaceae by Hermann Jacobsen, with pp. 589 and 1063 illustrations in black and white on 200 plates. Jena: Fischer Verl., 1970. M48.00.

As the title suggests the book deals with this vast subject in a very condensed, encyclopaedic way. It deals with all the known succulents with the exception of the Cactaceae. The book is divided into 2 sections, part 2 contains all the Mesembryanthemaceae, part 1 all the other succulents.

For easy and quick reference the genera are in alphabetical order. For the larger genera like *Adromischus*, *Aeonium*, *Agave*, *Aloe*, *Anacampseros*, *Caralluma*, *Ceropegia*, *Cotyledon*, *Crassula*, *Dudleya*, *Echeveria*, *Euphorbia*, *Haworthia*, *Huernia*, *Kalanchoe*, *Monanthes*,

Pachyphytum, *Pachypodium*, *Rhodiola*, *Sedum*, *Sempervivum* and *Stapelia* the division into sub-genera and sections has been given. In addition there is a key to the sections of the genus *Haworthia* and keys to the species of the genera *Alluaudia*, *Alluaudiopsis*, *Ceropegia* and the succulent species of *Peperomia*. To each sub-section of a genus the respective species are listed. With each species of the larger genera goes the number of the particular sub-section or paragraph, into which the genus has been sub-divided.

The descriptions of the species are very abbreviated in order to get as much information as possible into the limited space of this encyclopaedia. A loose card of abbreviations which of course can be carried forward from page to page makes the reading of the text very easy.

Part 2 of the book gives a shortened account of the taxonomy of the Mesembryanthemaceae by G. Schwantes in the revised form of G. Schwantes, H. Straka and H. D. Ihlenfeldt. It is also provided with the revised key to the genera of the Mesembryanthemaceae by Dr. L. Bolus.

For the genera *Argyroderma*, *Conophytum*, *Gibbaeum*, *Lampranthus*, *Lithops*, *Monilaria*, *Ruschia*, *Sphalmanthus*, and *Stomatium* the sub-division into sub-genera and sections has been given. In addition there are keys to the sections of the genera *Cephalophyllum*, *Cheiridopsis*, *Drosanthemum*, *Trichodiadema* and keys to the species of the genera *Aloinopsis*, *Astridia*, *Dinteranthus*, *Dorotheanthus*, *Dracophilus*, *Herrea*, *Juttadinteria*, *Khadia*, *Lithops*, *Machairophyllum*, *Meyerophytum*, *Namibia*, *Nananthus*, *Ophthalmophyllum*, *Rabiea*, *Rhinephyllum*, *Schwantesia and Vanheerdia*. The description of the species has been carried out as in part 1.

For recent descriptions of new species or new combinations and a few other plants not mentioned in the general text there are two appendices. Two extensive lists of synonyms separate for the Mesembryanthemaceae and the other succulents add even more to the value of this book.

For the reader with more detailed and deeper interests there is a long list of literature used by the author when compiling this book. Lists of old and new names for the areas where succulents occur, of societies for the study of succulents, plus a list of families which contain genera with succulent species add to the amount of information.

Last but not least, tribute should be paid to the many good photographs which will prove of greatest value for the identification of plants. Most valuable are the drawings to the sections in the *Euphorbias*, *Haworthias*, *Monadeniums and Gibbaeums*, and the photographs to the *Lithops* system.

Perhaps more emphasis should be placed on the importance of the capsules in the Mesembryanthemaceae. Illustrations of a greater number of capsules could greatly improve this part of the book. It seems that this aspect has been a little underestimated by the author. If one compares "Das Sukkulenten Lexikon" with the botanical information given in the old 3 volume "handbook", the improvements are considerable, especially in part 2. We nevertheless do not share the optimistic outlook of the publishers that with this book in hand, the correct identification of any succulent is possible without any problems. Further, we do not agree that *Testudinaria* is the current valid name for the genus *Dioscorea*. But thisi s of minor importance.

The volume is moderately priced.

We have to congratulate Dr. Jacobsen on this handsome work which provides the professional as well as the layman with such very able and comprehensive information on succulents.

Walter Wisura

JOURNAL OF SOUTH AFRICAN BOTANY

VOLUME 37 1971

INDEX OF PLANT NAMES

Note: Page references to new taxa are printed in bold type. An asterisk indicates an illustration.

INSTRUCTIONS TO CONTRIBUTORS TO THE JOURNAL OF SOUTH AFRICAN BOTANY

This Journal provides a medium for the publication of the results of botanical research primarily on the flora of Southern Africa, whether systematic, morphological, ecological or otherwise and whether carried out in South Africa or elsewhere. Papers on botanical subjects of special interest and application in South Africa may be included

Contributions must be original and should not be translations of previously published papers.

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Papers should be type-written, double spaced throughout on one side of the paper and with margins of at least 3 cm (1 inch). Footnotes and elaborate tables should be avoided. Latin binomials should be underlined once to indicate italics. All other marking of copy should be left to the Editor. The original, plus at least one carbon copy, must be submitted.

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Each paper should be headed with a concise informative **title** in capitals with the author's name below. This should be followed by the name of the institution, where the work was carried out, underlined and placed within brackets.

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Tables and **illustrations** should be on separate sheets. **Figures** and **graphs** should be in Indian ink on white card or Bristol board. Lettering for figures can be inserted by the printers in which case authors should indicate the desired lettering on the original figure lightly in pencil. The maximum dimensions available for figures are 18 cm × 12 cm (7″ × 4½″). Line drawings for blocks should be at least twice the size they will be when reduced for publication. All figures should be supplied with a scale. The most suitable method of indicating magnification is a scale line (in metric units) incorporated in the figure. Photographs for half-tone reproductions should be on glossy paper, clearly marked on the reverse side (in pencil) to indicate the top. Line drawings and half-tone illustrations are termed figures and should be numbered consecutively. Captions for figures should be typed on a separate sheet of paper.

TAXONOMIC PAPERS

Authors must adhere to the International Rules of Botanical Nomenclature. **Abbreviations** and **herbaria** must be cited in accordance with the most recent edition of Index Herbariorum, Pt 1 (The Herbaria of the World, 5th ed., 1964). When **new species** are described, the exact location of type material must be indicated. When proposing **new combinations** the full citation of the basionym is required. **Indented keys** with numbered couplets are preferred when dealing with a small number of taxa. **Bracket keys** should be used when dealing with a large number of taxa. When citing **synonyms** they should be arranged chronologically into groups of nomenclatural synonyms and these should be

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Bequaertiodendron magalismontanum (Sond.) Heine & J. H. Hemsley in Kew Bull. **1960**: 307 (1960).
Chrysophyllum magalismontanum Sond. in Linnaea **23**: 72 (1850). Type: Magaliesberg, *Zeyher,* 1849 (S, holo; BOL!, SAM!).
Zeyherella magalismontana (Sond.) Aubrév. & Pellegr. in Bull. Soc. bot. Fr. **105**: 37 (1958).
Pouteria magalismontana (Sond.) A. Meeuse in Bothalia **7**: 335 (1960).
Chrysophyllum argyrophyllum Hiern, Cat. Afr. Pl. Welw. **3**: 641 (1898). Syntypes: Angola, *Welwitsch* 4827, 4828, 4829 (BM!).
Boivinella argyrophylla (Hiern) Aubrév. & Pellegr. in Bull. Soc. bot. Fr. **105**: 37 (1958).
Chrysophyllum wilmsii Engl., Mon. Sapot. Afr.: 47 t. 16 (1904). Type: Transvaal *Wilms* 1812 (B†, holo.; K!).
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CITATION OF SPECIMENS

In the interests of uniformity contributors are requested to follow the recommendations of the Botanical Research Institute, Pretoria (Technical note: Gen. 4, Oct., 1967) by citing specimens according to the one degree grid system. Distribution data are given separately for each province and are arranged in the following sequences: South West Africa, Botswana, Transvaal, Orange Free State, Swaziland, Natal, Lesotho, Cape. Within each province degree squares are listed in numerical sequence, i.e., from west to east and from north to south. Whenever possible locality records should be given to within a quarter degree square. The collectors' names and numbers are underlined (printed in italics) to avoid confusion with the numbers of the degree squares, e.g.: NATAL–2829 (Harrismith): Cathedral Peak Forest Station (-CC), *Killick* 5127 (PRE); . . . CAPE–3418 (Simonstown): Hottentots Holland mountains, Somerset Sneeukop (-BB), Nov., *Stokoe s.n.* sub. SAM *56390* (SAM).

REFERENCES

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Davis, P. H. and Heywood, V. H., 1963. *Principles of Angiosperm Taxonomy.* Edinburgh and London: Oliver and Boyd.

Riley, H. P., 1960. Chromosome numbers in the genus *Haworthia. Jl S. Afr. Bot.* **26**: 139—148.